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BOTANICAL GAZETTE

EDITORS:

JOHN MERLE COULTER AND CHARLES REID BARNES

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JANUARY-JUNE, 1909

WITH TWENTY-FIVE PLATES AND ONE HUNDRED AND FIFTEEN FIGURES

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ERRATA

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P. 302, line 7 from bottom, for KCl read CaCl.

P. 326, line 5 from top, for distant read distinct.

P. 400, line 6 from top, after division insert reduction; and in line 7, delete a and reduction.

Volume XLVII

P. 69, footnote 1, for Ewart, A. L. read Ewart, A. J.

P. 144, last line, for Goveniana read Goweniana.

P. 170, footnote 24, for Leavitt, R. S., read Leavitt, R. G.

P. 347, line 6 from bottom, for cones read comes.

P. 423, no. 9, for Abisdia read Absidia.

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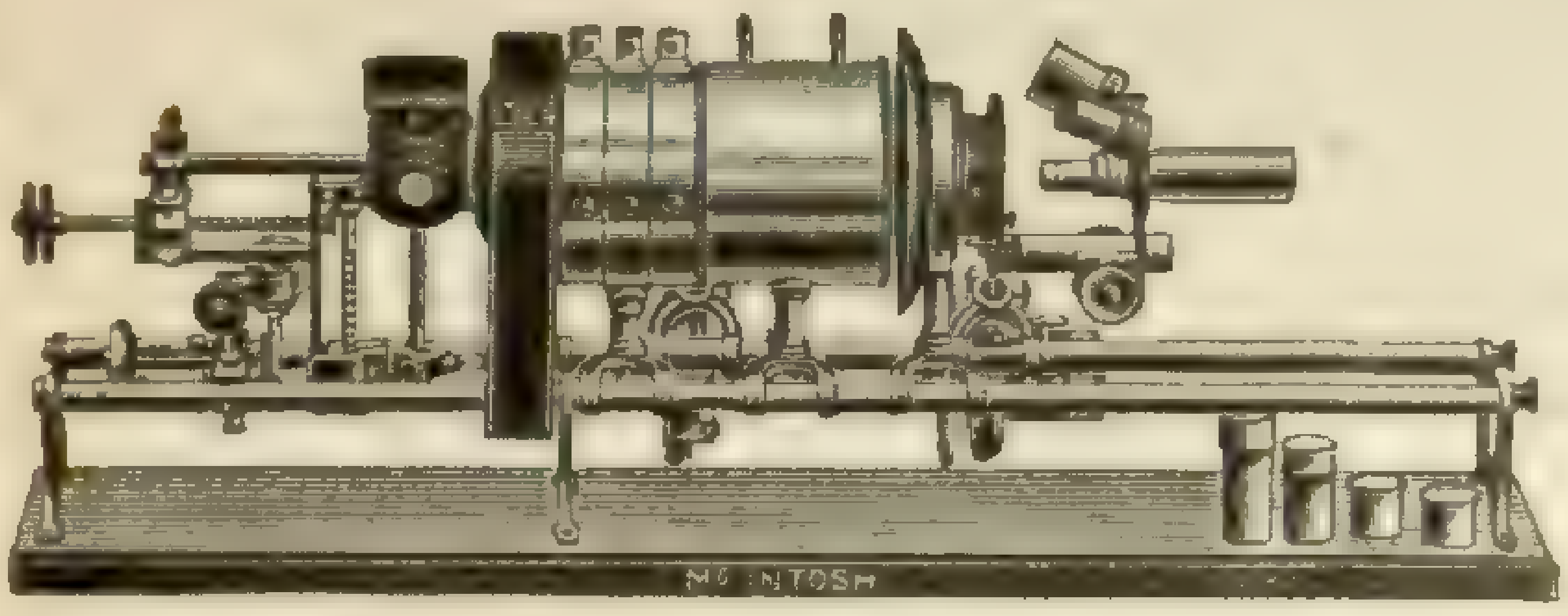

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BOTANICAL GAZETTE

JANUARY 1909

ON TRIPLE HYBRIDS

HUGO DE VRIES

Twin hybrids are produced when the pollen of *Oenothera Lamarckiana* or of one of its derivatives is crossed with the European subspecies of *O. biennis* or of *O. muricata.* These twins appear in about equal numbers and are constant in succeeding generations. One of them, *O. laeta,* is broad and smooth leaved; the other, *O. velutina,* is more hairy and has furrow-shaped leaves.[1]

Triple hybrids may be produced by combining this phenomenon with the hereditary qualities of *O. lata* and *O. scintillans.* Both of them originated in my garden from *O. Lamarckiana.* *O. lata* is female, its anthers are barren. *O. scintillans* is an inconstant species which repeats its type only in one-third or two-thirds of its offspring. Both of them, when pollinated by *O. Lamarckiana,* give a mixed progeny, only part of which is like the mother.[2]

In order to get triplets, therefore, we have to cross *O. lata* or *O. scintillans* with some species which will split them into *laeta* and *velutina* (as it would do *O. Lamarckiana* itself or some others of its mutant species), and which, moreover, does not prevent them from repeating their own type in their progeny. The triplets will then be *O. laeta, O. velutina,* and *O. lata.* The first two will drop the special character of the mutant-parent (BOT. GAZ. *l. c.* 403), but all three will be intermediate hybrids between *O. Lamarckiana* or *O. lata* and the species used as the other parent.

I found that *O. strigosa* Rydberg, *O. Hookeri* T. and G., and the common American subspecies of *O. biennis* L. comply with these requirements. The experiments to be described in this article are limited to the effects of their pollen on *O. lata* and *O. scintillans.*

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[1] BOT. GAZETTE **44**:401–407. 1907.

[2] *Die Mutations-Theorie.* Vols. I and II.

O. strigosa Rydb. has very small flowers, of the size of those of *O. muricata*, but in less dense spikes. They open their anthers two or more days before unfolding the corolla, and the pollen comes in contact with the whole outer surface of the stigma and causes fertilization. The leaves are bluish green and furrow-shaped, and the tip is bent sideways. The tops of young shoots, when seen from above, therefore, present the aspect of a wheel with spokes all curved to the left or to the right. This striking feature is repeated, though somewhat reduced, in all of its hybrids and causes them to be easily recognized. I collected seed in the Yellowstone Park in 1904. Another lot was kindly sent to me by Mr. T. D. A. COCKERELL from Boulder, Colorado. Of both strains I have since cultivated two generations.

In crossing *O. strigosa* with *O. Lamarckiana*, twins arise which combine the characters of *laeta* and *velutina* with those of *strigosa*. They differ more widely from one another than do the twins of any other cross I have studied up to this time. The *velutina* is almost like the *velutina* of *O. muricata* × *Lamarckiana*, but has the bluish tinge, the more pointed leaves with bent tips, and the wheel-shaped tops of the young shoots described above for *O. strigosa*. The *laeta* from the *strigosa* cross is a very stout plant with very broad leaves (6^{cm}), blunt at the apex and indented at the base, with smooth surface, and bright green. The flower buds are more narrowly conical than those of *velutina*, the flowers open more widely, the fruits are conical with four sharp and protruding teeth, whereas those of *velutina* are blunt and short. By this mark and by the somewhat narrowed neck of the fruits of *velutina*, the two forms are most easily distinguished when flowering is over. The *laeta* is usually poor, but the *velutina* is rich in pollen.

In contrast to the species previously dealt with, *O. strigosa* produces twins from *O. Lamarckiana* when used as male parent as well as when used as female parent. In these reciprocal crosses both of the twins are identical.

The twins produced by *O. strigosa* from *O. scintillans* and from *O. lata* comply with the description given. They cannot be distinguished from them externally, even when cultivated in large and pure lots.

O. Hookeri T. and G. is a Californian species and is also found in Texas.[3] I collected seeds in the vicinity of Berkeley, California, and another lot was sent to me from Riverside by Mr. FRED M. REED. It is a striking species, even more beautiful than *O. Lamarckiana*. The flowers are of the same size, protruding their pistils high above the anthers; but the petals are more deeply emarginate at the tip, nearly obcordate, and a paler yellow. The plant is hairy and reddish, and the leaves (especially those of the rosette) are long and narrow.

With *Lamarckiana* it produces twins identical in both reciprocal crosses and both of them as large-flowered as the parent species. The *laeta* is bright green, with smooth leaves and slender flower buds. The *velutina* is hairy and reddish, with furrow-shaped leaves and thick buds. It flowers more profusely and resembles *O. Hookeri* almost exactly, but is stouter, with dense and richly flowered spikes.

The twins derived by *O. Hookeri* from *O. lata* cannot be distinguished externally from those derived from *O. Lamarckiana*.

The American subspecies of *O. biennis* used for my experiments was collected by me in 1904 at Chicago, near Jackson Park. It seems to be the same form as that which is most common in the eastern states. Other subspecies I have collected in Pennsylvania, Kansas, Missouri, and elsewhere. All of them are quite different from the European form, which is the one used in my *Mutations-Theorie* and in my article on twin hybrids (BOT. GAZETTE *l. c.*). A systematic treatment of these numerous forms is still wanting, and therefore I will provisionally designate my strain by the name of its source and call it *Chicago*. Its most curious quality is that of producing twins when combined as a male parent with *O. Lamarckiana* and not when crossed with the pollen of this species. In this respect it is exactly opposite to the European *O. biennis*, and therefore very useful.

The *O. biennis* from Chicago is a taller plant, more richly branched, and darker green than the European form. Its flowers are much smaller, sometimes reaching the size of those of *O. muricata*, but deeper yellow. The stigma is surrounded by the anthers which open early in the bud. The *velutina* and *laeta* which it produces from *Lamarckiana* can hardly be distinguished from those produced by the European *O. biennis*, although the leaves are narrower and darker green. I cultivated this strain during three succeeding generations.

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[3] *Oen. Hookeri* T. and G. = *Onagra Hookeri* Small = *O. biennis hirsutissima* Gray, Bot. Calif. See H. M. HALL, A botanical survey of San Jacinto Mountain. Univ. Calif. Publ. Bot. 1:98. 1902.

O. scintillans and *O. lata* are the mutant species described in my *Mutations-Theorie*. The *scintillans* used originated from *Lamarckiana* seed of 1889 which was sown in 1895. In 1906 I had the fourth generation from continued pure self-fertilizations and used it for my cross. From this same strain the *lata* used in the experiments of this article arose as a mutant in 1901. It was artificially fertilized. My crosses were made with specimens of the second and third generation of its progeny.

I will now describe the crosses from which the triplets resulted.

Oenothera scintillans × *strigosa*.—This cross was made in July, 1907, between two biennial specimens. It yielded a small lot of seed which was sown the next spring. From it arose 36 *laeta*, 21 *velutina*, 15 *scintillans*, and one *lata*, altogether 73 plants, most of which flowered during the summer. The *laeta* and *velutina* agreed with the description given above; the *lata* was a mutant. The *scintillans* were intermediate hybrids, which had the habit and leaves of the mother parent, or nearly so, but small flowers with the anthers surrounding and touching the stigma like the father. I fertilized all three forms with their own pollen and intend to sow the seed next year.

Oenothera lata × *strigosa*.—This cross was effected in 1905, both parents being annual specimens. I used different plants of *lata* and sowed the seed of one cross in 1906, of another cross in 1907, and a third lot in 1908. I got the following results:

Year	Number of specimens	Percentage *laeta*	Percentage *velutina*	Percentage *lata*
1906....................	41	36	59	5
1907....................	47	49	40	11
1908....................	270	27	34	38
Total..................	358	40	33	27

The *laeta* and *velutina* were the same as those from the cross with *Lamarckiana*. I sowed self-fertilized seed from plants of 1906 in 1907; the mothers were *velutina* and gave 113 children, most of which flowered. All of them were *velutina*. In 1907 I self-pollinated some *laeta* and some *velutina* and got 80 and 45 seedlings respectively. The first were all *laeta*, the second lot was uniformly *velutina*. Of each lot 25 specimens were preserved after the sorting period and observed during the time of flowering and ripening of their fruits.

The *lata* were intermediate between *O. lata* and *O. strigosa*. In 1908 I cultivated one half of them in the open and the other under an open glass-covering, both of them with cultures of ordinary *lata* under the same conditions for comparison. The *lata* from the *strigosa* cross had narrower leaves but with the rounded tips; the bracts were broad but less bent downward. The flowers were much smaller than those of the mother, but somewhat larger than those of the father. Their shape resembled that of *O. strigosa*, but the stigma showed, although in a lessened degree, the peculiar hand-shaped form of the ordinary *O. lata*. The anthers touched the stigma, but only with their lower halves. The flower buds were broad, and the tube was relatively short. In all these points and in the other characters the *lata* hybrids were strikingly intermediate between the two parents. Even the bent tips of the young leaves were to be seen, and at once revealed the father. But the most interesting feature was that of the pollen. *O. lata* is purely female, while *O. strigosa* has the ordinary supply of pollen. The hybrids showed some pollen and a relatively small number of fertile grains. These were, during ordinary weather, insufficient for fertilization, even if the pollen of many flowers was brought upon one stigma. But there were individual fluctuations, and so I succeeded in getting self-fertilized fruits on at least one specimen.

Oenothera lata × *O. biennis Chicago*.—This cross was made in 1905, both parents being annual. Two specimens of *O. lata* were used. I sowed their seed in different lots in the three succeeding years and had the following results:

Year	Number of specimens	Percentage *laeta*	Percentage *velutina*	Percentage *lata*
1906	33	27	70	3
1907	78	34	29	37
1908	167	36	28	35
Total	278	35	34	31

The *laeta* and the *velutina* were of the description already given. I sowed the self-fertilized seed of 1906 in 1907 and 1908 and had four lots of the second generation. The lots of the first included 69 and 139 individuals, all of which were *laeta;* the sowings of the other strain extended over 38 and 158 samples, all of which were *velutina.* Both of the twins thus complied with the rule of constancy in the second generation. From the lots of 1907 I cultivated in 1908 a third generation comprising 70 children of *laeta* and 90 of *velutina;* both lots were once more uniform and similar to their parents.

The *lata* individuals of this cross were almost similar to those of *O. lata* itself. However, they had the smaller flowers of *O. biennis,* with the self-fertilizing position of the stigma, and the long lobes of the father. Their flower buds were intermediate between those of the two parents. In 1906 and 1907 the anthers seemed wholly barren; but in 1908, during the very warm last days of July, they yielded some pollen, which was used partly for self-fertilization, partly for crosses.

O. lata × *Hookeri.*—This cross is the most interesting of all the crosses with *O. lata,* since its *lata* hybrids are almost as rich in pollen as any other evening primrose. This enabled me to study the second generation of the *lata,* which, in contrast to that of the *laeta* and the *velutina,* repeats the splitting. The yield of the pollen was small in the unfavorable summer of 1907, but large during the hot days of July and August, 1908.

I have made this cross twice, in 1905 and 1907; the parents were annual specimens. I had the following results in the first generation:

Year	Seed of	Number of specimens	Percentage *laeta*	Percentage *velutina*	Percentage *lata*
1907....................	1905	51	53	39	8
1908....................	1905	229	45	47	8
1908....................	1907	72	49	28	22
Total..............		352	47	42	11

Here also the *laeta* and *velutina* were the same as those from the cross with *Lamarckiana.* I sowed some self-fertilized seed of the *velutina* of 1906, partly in 1907 and partly in 1908, and cultivated from each lot 60 specimens, all of which repeated the *velutina* characters.

The *lata* specimens also were cultivated from seed of 1906 in both succeeding years. Their flowers were as large as those of both parents and intermediate in the tinge of the yellow, the *Hookeri* being paler yellow than the *Lamarckiana* and its *lata*. The anthers did not reach the stigma, which was often hand-shaped. The spike was much denser than that of *Hookeri* but thinner than that of the mother. Stem, veins, and calyx were reddish; and leaves were narrower than in *O. lata*. In all these and in other characters the plants were strikingly *lata*, but with the addition of the differentiating marks of the *Hookeri*.

The self-fertilized seed of the *lata* plants of the first generation gave a mixed progeny, consisting of *velutina* and *lata*, both resembling the types of the first year. No *laeta* specimens were produced. The numbers were the following:

Year	Number of seedlings	Percentage *velutina*	Percentage *lata*
1907..........	53	85	15
1908..........	134	81	19
Total.....	187	82	18

From the experiments described the following table may be compiled:

TRIPLE HYBRIDS AND THEIR SUCCEEDING GENERATIONS

Mother	Father	First generation Percentage	Second generation	Third generation
O. scintillans	× O. strigosa.........	49 laeta 29 velutina 21 scintillans		
O. lata	× O. strigosa...........	40 laeta 33 velutina 27 lata	80 laeta 158 velutina	
O. lata	× O. bien. Chicago.....	35 laeta 34 velutina 31 lata	208 laeta 196 velutina	70 laeta 90 velutina
O. lata	× O. Hookeri...........	47 laeta 42 velutina 11 lata	120 velutina 82 per cent. velutina 18 per cent. lata	

QUADRUPLE HYBRIDS.—The discovery of twin and triple hybrids naturally suggests the idea of the possibility of a hybrid quartette. As a matter of fact the experiments did the same. In the case of *O. lata* × *O. biennis* from Chicago a fourth type appeared in one specimen, and in that of *O. lata* × *O. Hookeri* in two specimens. These three plants belonged evidently to the *lata* type, but combined with this the smooth, broad, and bright-green leaves of the *laeta*, whereas all the other *latas* of these crosses had gray and furrow-shaped leaves like the *velutina*. The *lata-laeta* of the first cross was sufficiently fertile, but of two of the *Hookeri* cross one had barren anthers and the other only some spare pollen in comparison with the rich supply of pollen in the other *lata* plants of this cross. In this respect, therefore, they also showed the character of the *laeta* type.

It would seem probable that the *lata-laeta* should be produced in the same number as the other *lata*, or *lata-velutina* as we could now call it. But then the *laeta* itself often appears in too small numbers. The cause of this phenomenon has still to be investigated.

Summary

1. Triple hybrids are produced in crosses of *Oenothera scintillans* and *O. lata* by such species as produce twins from *O. Lamarckiana*.

2. The species investigated are *O. strigosa* Rydb., *O. Hookeri* T. and G., and one of the American subspecies of *O. biennis*.

3. Of the triple hybrids, two are the same as the twins from the corresponding *Lamarckiana* crosses and bear the characters of *O. laeta* and *O. velutina* combined with those of the other parent.

4. The third type resembles the mother (*O. lata* or *O. scintillans*), but in its special marks is also intermediate between its parents.

5. The *laeta* and *velutina* are constant and uniform in their succeeding generations, so far as experience goes. In this respect they follow the rule for the twin hybrids of *O. Lamarckiana*.

6. The *lata*, however, in the only case tried, repeated the splitting after self-fertilization, producing, however, only *lata* and *velutina*.

7. It seems probable that the whole progeny of the crosses named should split up into two equal parts, *laeta* and *velutina*, and that each of them should produce a certain percentage of *lata*. In this way quadruple hybrids would arise.

BOTANIC GARDEN
AMSTERDAM

PERIODICITY IN SPIROGYRA

W. F. Copeland

The object in beginning these studies with Spirogyra was to get notes on the rearing of species and to see how far they could be changed by conditions. With this end in view 100 aquaria were started and soon contained puzzling results. To interpret these and to get on with the experiments, it soon seemed desirable, if not necessary, to know how Spirogyra lives under natural environment. For this reason the major part of my time was given to a consideration of this plant out of doors. An attempt has been made to repeat all observations and experiments under as great a variety of conditions as possible in an ordinary biological laboratory. When field-work was not practicable or necessary, laboratory work was resumed. In this way scores of experiments have been in progress from the beginning.

After this work had continued for some months, considerations were given to conditions appearing with some regularity whether Spirogyra was being studied under natural or under artificial environment. As a possible constant condition, it was finally decided to give special attention to the subject of periodicity. In this paper only those experiments will be mentioned which seem to have some bearing on this subject. Although laboratory studies are of minor importance in the subject of periodicity, in the present discussion they will appear first.

I take this opportunity to express my obligation to those who have in any way aided me in the present study. It is a pleasure to thank Dr. C. F. Hodge, who suggested the problem, for his help and criticism; Helen Reinherr Copeland for help in identification of species and preparation of material for microphotographs; O. W. Mills, Millbury, Mass., for collecting much valuable material in that locality; and Dr. O. P. Dellinger, Worcester, Mass., for helpful suggestions and criticisms. The following persons have sent me conjugating specimens from more distant localities: W. D. Hoyt and I. F. Lewis of Johns Hopkins University; B. A. Place, Iowa

Wesleyan University; S. G. WINTER, Illinois Wesleyan University; and W. A. MATHENY, Sardis, Ohio.

Review of literature

In 1803 VAUCHER (**6**) tells of his attempt to work out the life-history of the Conjugatae. For this purpose the genus Spirogyra was used and especially the species which MÜLLER had previously described as *Conferva jugalis.* VAUCHER'S observations were made in the spring and it was found that this species would fruit and disappear as early as February 15 and as late as March 20. The zygospores which he had collected germinated July 15, and all seemed to germinate on the same day.

A history of the British freshwater algae by HASSALL (**3**) appeared in 1857. This well-known work contains descriptions of 42 species of Spirogyra under the name Zygnema. A single hint is given as to the time of year when conjugation takes place; namely, "The species of this group of confervae may be found in a state of conjugation during the entire spring, summer, and autumnal months, but more abundant in the spring."

In 1874 *The freshwater algae of the United States* by WOOD (**9**) was published in the Smithsonian Report. Speaking of the Zygnemaceae he says: "The family under consideration is among the commonest and most widely diffused of all the freshwater algae. They may be found in greater or less abundance at all seasons, but the spores appear to be formed only in the spring and early summer, at least these are the only times at which I have found fertile filaments. In the neighborhood of Philadelphia I have collected them in excellent condition as early as the beginning of April and as late as the latter part of June. Further south conjugation of course commences earlier, and fine specimens received by myself from Mr. CANBY were collected by him in Florida in February."

The work of PAUL PETIT (**5**) entitled *Spirogyra des environs de Paris* appeared in 1880. No general statement is made regarding the fruiting season of this genus, but, with one exception, dates are given with the description of the different species. These dates show that 20 of the 36 species described matured during March, April, and May; and all except two had matured by July. These were found in fruit from July until October. One species fruited in April and May and again in October.

Since 1880 a number of papers relating to Spirogyra have appeared, but only a few of them give any facts that can be used in a study of periodicity. BENNETT and MURRAY (**1**) write: "Germination sometimes takes place while still in the mother cell; but most commonly both filaments perish after conjugation, with the exception of numerous zygospores which fall to the bottom. These remain dormant through the winter . . . . germinating in the spring . . . . instances are recorded of filaments persisting through the winter. HOFMEISTER states that the growth of Spirogyra is intermittent."

The following case is reported by W. and G. S. WEST (**7**): "We have melted out of the ice from Micham Common, Surrey, excellent examples of *Spirogyra catenaeformis* in conjugation, the vitality of which was in nowise impaired."

The few scattered remarks given include all the notes the writer has been able to gather from papers published before 1905. In this year a few papers appeared which had a more direct bearing on the subject at hand. These seem to be the pioneer publications on the subject of algal periodicity. In indicating some of the "problems of aquatic biology" FRITSCH (**2**) calls attention to the fact that different bodies of water, often far apart, will have the same dominant and often the same subordinate vegetation; also that a plant may be very abundant one month and almost, if not entirely, absent the next month. An intimate relation was found to exist between the relative abundance of an alga and its period of reproduction; the formation of the sex organs frequently preceding the disappearance or diminished abundance of a given species. FRITSCH writes: "In some cases no doubt these features (maximum abundance and period of reproduction) are influenced by the periodically recurring factors such as the rise of temperature and the increase in the intensity of light in the spring; so that the maximum abundance and period of reproduction are definite phenomena."

Another paper on the subject of algal periodicity appeared in 1905. So far the publications mentioned have had to do only with freshwater algae; for that reason it is well to call attention to studies made on marine forms. While at work on Dictyotaceae, WILLIAMS

(8) discovered that Dictyota had definite periods for the development of its fruit. This is well explained in his introductory paragraph: "While studying the development of the sexual cells in Dictyota, the interesting discovery was made that the process was practically simultaneous, not only for a given plant but for all the plants of the locality."

This work by WILLIAMS was done at Bangor, Wales, and at Plymouth, England. During the summer of 1906, observations were made on the same plant at Beaufort, North Carolina, by W. D. HOYT (4): "It was found at Beaufort, also, that this alga produced its sexual cells in regular, periodic crops. . . . . One observation is interesting in this connection. A female plant kept in the laboratory for nearly two months and then examined showed sori only slightly less advanced than those on plants growing in the harbor. . . . . This result is similar to the one observed by WILLIAMS but goes a step farther in showing that periodicity is transmitted to new structures formed from the original plant, even where these are not subjected to alternating conditions. . . . . It still remains to be seen whether the periodic habit can be transmitted through the protoplasm of the egg."

Spirogyra under artificial environment

In the laboratories in which these experiments were conducted, windows were used which faced toward the northwest, northeast, and southeast. Whenever a new line of investigation was begun, three sets of aquaria of different sizes were prepared. One set was placed in a northwest, one in a northeast, and one in a southeast window. The conditions made use of in the three sets of experiments were the same with the exception of a few degrees in temperature and a difference in light intensity. Other experiments were conducted which had nothing to do with conditions of temperature and light.

In the first experiments Spirogyra was brought into the laboratory and small amounts placed in aquaria filled with water from the pond from which the plant was taken. In some cases the plant was washed before being transferred to the aquaria, in others it was not.

A second group of experiments contained the same conditions with the exception of the culture medium. In this group attempts were made to repeat the experiments while using tap instead of pond water. As a result, it was found that the aquaria with tap-water were as satisfactory, and, in most cases, much more so than those with pond water. Hence tap-water aquaria were used as controls.

It is well to note concerning this point that the tap-water was from reservoirs which were in turn supplied by small brooks and surface drainage. In many cases the pond water was taken from ponds supplied by brooks which drained the reservoirs just mentioned.

I next tried a group of experiments for the purpose of fixing some value to the use of plant food solutions for the investigation at hand. Knop's solution was most frequently used; however, Sachs's solution was employed in a great many experiments and in most cases simultaneously with Knop's. In comparing aquaria with and without food solutions, no general rule could be established. On the whole, however, the writer is inclined to favor at least a weak food solution. Knop's solution as low as 0.04 per cent. gave favorable results.

A long list of experiments was prepared in which rain and distilled water were used; and in others melted snow. Some of these were not disturbed after being placed in their respective windows. Others were left in these media for periods varying from one to ten days and then changed to a weak food solution (usually 0.05 per cent.), and this was raised by degrees to 0.2 per cent. where it was allowed to remain. In this group care was taken to select Spirogyra from different localities. Specimens were obtained from swift water, from slow-running brooks, and from small quiet pools and ponds where very little disturbance was possible. Notes on these experiments show that no particular advantage was gained by using these media.

From the first the aquaria located in the southeast windows were shorter lived than either of the other sets of aquaria. It will be remembered that the only difference in conditions was a slight difference in temperature plus a difference in light intensity. Experiments were now conducted in order to try the effect of shading the cultures. Tissue paper of different colors was used for this purpose. The best results were obtained when the aquaria were not shaded above the surface of the water. After scores of experiments the best results were obtained in the following way: when an aquarium was started, it was shaded with black paper; after two weeks, this was changed to yellow; and after another two weeks the shading was not used at all. This was a decided advantage to the aquaria in the southeast windows. While the effect was not so noticeable in the other laboratories, the results were sufficient to justify this method in all the windows. It is not to be understood that tap-water aquaria were the only ones used with a shade. On the other hand, snow, rain, distilled water, and food solutions were used in every case. The same applies to the following series of experiments.

Up to this time no attention has been given to the substratum, nor to other plants with which Spirogyra is most frequently associated in its natural habitat. For this group of aquaria soil, débris, and plants, for the most part, were used from the immediate locality from which the specimens were taken. In some cases the soil was first sterilized.

Among the plants which seemed beneficial to Spirogyra, none proved more helpful than Oedogonium. In fact in every aquaria in which Spirogyra lived for several months or a year, Oedogonium was invariably present and often the predominating alga. The Oedogonium could usually be found attached to the sides of the jar or floating at the surface, thus shielding the Spirogyra from too much sunlight. Chara supplied to the aquaria was helpful so long as it was not too abundant. In some cases where aquaria were thus started, the Chara died out after two or three months and was followed by an abundant growth of Oedogonium, and later by Spirogyra. In the field, masses of Spirogyra were often collected among water cress, but in no case was a good growth of Spirogyra obtained in an aquarium with this plant. A number of jars were supplied with oak leaves taken directly from the trees where they had remained all winter. To other aquaria pieces of charcoal were added. Both of these factors seemed beneficial and in most cases excellent cultures of Spirogyra were obtained which lasted until conjugation had taken place.

Spirogyra under natural environment

Field-work was begun early in April. At this time 400 aquaria of all sizes were in use and 100 of them contained excellent cultures of Spirogyra which had been under cultivation for two months. On

April 27 *S. quadrata* was found conjugating abundantly. This one was followed by others until twelve different species had matured and disappeared. At first all material was brought to the laboratory in small jars and then examined, but this method was by no means satisfactory. A microscope together with a crude temporary stand was added to my collecting outfit, and an examination of all material was made on the spot. There are so many chances of collecting worthless material that no other method was found which would give definite results.

The first task was to locate Spirogyra in a number of different localities with different conditions of environment. Accordingly a few localities were selected varying from a few rods to twelve miles apart. Within these regions 40 different places were selected which could be visited frequently and studied with care. Some were in open places, while others were in deep shadow; some were in pure running water, others in filthy stagnant pools; some with numerous other algae, others almost alone; and under many other conditions.

For identification of species some of the material was usually killed in the field as soon as collected. From 2 to 4 per cent. solution of formalin was used for this purpose when larger masses were killed, but in most cases chromacetic solution was used according to the formula given in CHAMBERLAIN'S *Methods in plant histology*, p. 139 (chromic acid 1^{gr}, glacial acetic acid 4^{cc}, water 400^{cc}). Several stains were used, but Haidenhain's iron-hematoxylin was most satisfactory. Some of the specimens stained in this way were afterward mounted in glycerin, others in balsam, and others in Venetian turpentine. I found the balsam more satisfactory than the turpentine, but excellent preparations were obtained by using the Venetian turpentine method recommended by CHAMBERLAIN (stain with magdala red and anilin blue and mount in Venetian turpentine). Stained preparations in glycerin were most quickly obtained by taking the material as soon as washed from the chromacetic solution, transferring it to a 10 per cent. solution of glycerin to which was added 2 or 3 drops of Ehrlich's blood stain, and allowing it to concentrate. In some cases the stain obtained by this method has been permanent, in others it has faded after a few months. This method of preparation has been used with much success by F. N. DUNCAN and O. P. DELLINGER, of this laboratory, for animal tissue.

Periodicity of species studied

For the purpose of identifying the different species, the following authors were consulted: VAUCHER (**6**), WOOD (**9**), PETIT (**5**), and WOLLE (**10**). A brief account of the fruiting season of the different species will be given below.

Spirogyra inflata (Vaucher) Rab.—VAUCHER reports this species in fruit from February 20 to March 19. PETIT gives April–May. Unfortunately I was not able to find it except in a single locality. This was in a small pond covering an area of perhaps $1000^{\text{sq. ft}}$. The surface was well covered with algae and floating débris of small sticks and grass. This species was found floating on the water together with *S. catenaeformis* and *S. calospora.* On May 2 all three species were found in a state of conjugation interwined with each other. No indication of *S. inflata* was found after May 12, although this pond was visited frequently during the summer and fall.

Spirogyra quadrata (Hassall) P. Petit.—This is the *Zygnema quadratum* of HASSALL. PETIT gives the fruiting season as April–May. The writer studied this species in eight different localities, varying from a few rods to twelve miles apart, but under no great variety of conditions. In every case it was found in quiet surface-water pools or streams which were entirely dry by the middle of July. All the eight places were in low pastures or meadows and specimens were collected from among dead grass and leaves. *S. quadrata* was found fruiting abundantly April 27, and within a week the eight places mentioned above were visited and found in about the same state of conjugation. By May 5 the Spirogyra at two localities had fruited abundantly and had passed the maximum of conjugation. By May 12 this was true in every case and no fruiting material was found after May 19. The temperature of the water recorded at each visit to the different ponds gave a range of 10–25° C. It was very difficult to collect any vegetative filaments of this species after the period of maximum conjugation had passed.

Spirogyra calospora (Cleve).—WOOD found this species fruiting in a ditch in a meadow late in April, and as late as May 25 in the "neck" below Philadelphia. The season given by PETIT is April–May, and the habitat "ditches in low ground and swamps." For this species the present paper includes notes from observations of five different ponds and one brook in different localities, and including a greater variety of conditions than those described for *S. quadrata*. Early in April the plant in question was growing abundantly and continued in increasing abundance until about the second week in May. In two of the ponds the disappearance was by no means rapid. A few scattering filaments were found May 6 and the last June 4. The average temperature was 7–14° C. In the pond in which most fruiting material was found the temperature ranged from 7 to 11° C at the time of maximum conjugation.

Spirogyra Hantzschii Rab.—In 1906 fruiting material was collected first on April 28, and, with one exception, no fruiting material was gathered after May 23. In the fall of 1905 this species was found in active vegetative condition in three localities. Examinations were made frequently during the fall and, when the ponds were free from ice, during the winter. This species lived beneath the ice and in two of the three localities the plant did not come to the surface at the time of conjugation, but was collected from the débris at the bottom of the ponds. Temperature of the water varied from 12–28° C. There was no great range of habitat; generally in shallow ponds near the mouth of a small stream, and more or less protected from the midday sun.

Spirogyra mirabilis (Hassall).—This species is described by HASSALL and also by PETIT as producing spores without conjugation and by no other method. WOLLE states that lateral conjugation is more frequent than scalariform. I was not able to find this species in fruit in the pond from which this material was taken. It was brought into the laboratory in the vegetative condition April 2 and within a week was fruiting in several aquaria. On May 7 a few filaments with scalariform conjugation were found; all other spores were formed in cells where no conjugation had taken place. Comparatively few cells formed spores and very few cells conjugated. PETIT gives March–July as the fruiting season. In the material mentioned all fruiting specimens had disappeared in all the aquaria by the second week in June.

Spirogyra Jurgensii (Ktz.).—This species was found in fruit in the neck of a small pond May 4, 1906. In the same locality were found vegetative filaments of *S. Hantzschii* and Oedogonium, besides sticks, dead grass, rusted wire, and tin cans. The algae mentioned were found here in small patches January 8, and were visited at least once each week until June, at which time no algae of any kind were present. The fruiting specimens were most abundant when the temperature averaged about 12° C., and lasted about a week. No fruiting specimens were found after May 25. Petit gives the conjugating season as April–May.

Spirogyra catenaeformis (Hassall) Ktz.—This species, so far as I know, has not been reported for this country, and is so placed because it corresponds so closely to the descriptions in the works of Hassall and Petit. The latter author gives the fruiting season as April–May, and the habitat "very humid ditches, wooded ponds, etc." The first fruiting material was collected May 4 and the last May 22. It was found in two localities about two miles apart. One was a shallow ditch and the other was in cow tracks near a small stream. The period of conjugation was the same for both localities. The temperature of the water ranged from 14 to 17° C. This species was found with *S. dubia* in one pond and with *S. inflata* and *S. calospora* in another pond.

Spirogyra varians (Hassall).—This plant was studied in five localities from one to eight miles apart. In one case the water was rather swift and the Spirogyra was fruiting wherever it happened to lodge against a support. The other localities were shallow ditches and ponds. The first fruiting material was collected May 2, and the last May 23. In all localities except that in swift water this species fruited abundantly. The average temperature of the water was 8–12° C.

Spirogyra longata (Vaucher).—For this species my observations were confined to two ponds about one mile apart. In one *S. longata* covered an area of perhaps $200^{\text{sq ft}}$ and in the other fully 100 sq. rods of surface. In both ponds the plant in question was well exposed to bright sunlight, receiving its main protection from numerous algae which were present. The temperature of the water ranged from 20 to 25° C. and the depth of the water from a few inches to several feet. VAUCHER says that this species conjugates from February 20 to April 12; PETIT gives April–May. In the ponds mentioned this species appeared in July and with increasing abundance until early in August. The first fruiting specimens were collected August 2, and the last August 21, and neither vegetative nor conjugating filaments as late as September 1.

Spirogyra Lutetiana (P. Petit).—I was not able to identify this species except in a single locality. Its habitat was a small open ditch in a meadow unprotected from the sun. PETIT gives the fruiting season as March–May. The only date at which I found it in a state of conjugation was October 14, and when collected it had all the appearance of being old material which had fruited earlier. This may have been a week and it may have been a month.

Spirogyra dubia Ktz.—Concerning this species WOOD writes: "I have found this species fruiting abundantly in May. When in this condition it forms a mass of dirty yellowish-green." WOLLE agrees as follows: "Fruiting abundantly in May; forming dirty yellowish-green masses." I have found this species in fruit in seven different localities. The first date for each was as follows: May 1, May 2, May 21, July 31, July 31, August 10, and August 10. Those fruiting in May were found in rather sluggish streams and in water varying in depth from one to four feet; those fruiting in July and August were in cattle tracks and in a small ditch. The conjugating period in the spring lasted about four weeks; in the summer the period was about two weeks. The temperature of the water in the former ponds varied from 12 to 18° C.; in the latter places from 22 to 28° C. All seven localities were situated where the plant was protected from direct sunlight for a part of the day.

Spirogyra orthospira (Nägeli).—I had an excellent opportunity to watch the life-history of this species in a small pond of about 100 sq ft in area, two to four feet deep, and well shaded with low alders. The surface of the pond was entirely covered with Spirogyra to a depth of several inches. On May 22 it was found to be fruiting abundantly both at and beneath the surface. It reached its maximum about the second week of June, and by June 30 either vegetative or conjugating filaments could be found only by examining the débris at the bottom of the pond.

General conclusions

In forming conclusions concerning whether any given plant passes through a series of regular recurring phenomena, it is well to withhold positive conclusions until the plant in question has been carefully observed for a number of successive seasons. This method of approach becomes more complicated, but at the same time safer, if the plant can be studied from a number of varying conditions of environment. However valuable external conditions may be in effecting any given phenomenon, it seems well not to overlook whatever influence may be due to internal conditions. There may be conditions that cannot be seen, felt, weighed, or measured, that initiate and support even the simplest plants through a series of complicated phenomena. Notes on Spirogyra for this region seem to credit much influence to internal conditions. Here were forty different places in which this plant appeared, matured, and disappeared, in a single season. Without a single exception the disappearance was immediately preceded by a period of conjugation. Special importance is given to the fact that in no case did all of the filaments enter into spore formation either with or without conjugation. It is to be further noted that both the vegetative and conjugating filaments disassociated almost at the same time and disappeared, even from places where this plant was abundant over comparatively large areas of surface.

Of the twelve species studied, ten were in fruit in May, and in every case the maximum abundance of conjugation occurred within this month. In a few places more than one species was in fruit at the same place and time, but usually if several forms grew together they conjugated at different times, their period of maximum conjugation succeeding one another at intervals ranging from one to two weeks. For example, early in March, within a distance of forty rods, four species of Spirogyra were found growing together at three different places at the edge of a slow brook. In two of the three places Spirogyra was very abundant and covered an area in each of about $200^{\text{sq ft}}$. Probably all had had the same source earlier in the year during high water, but remained distinct until all had disappeared in June. No fruiting material was found in either of the larger patches; two of the four fruited in the smaller one, but not at the same time.

S. Jurgensii was found in fruit May 1–May 15; *S. dubia* was found fruiting May 21–June 4.

Under the description of *S. inflata* mention was made of the fact that on May 2 this species together with *S. calospora* and *S. catenaeformis* were found in fruit at the same time and place. It ought to be noted, however, that *S. inflata* had passed its period of maximum conjugation and that there were comparatively few filaments of either of the other two species. No *S. inflata* was found after May 4, but from this until May 22, *S. catenaeformis* was abundant. In giving a description of the latter species it was noted that this form was found fruiting abundantly at the same time and quite near *S. varians*. I did not find the two species intermingling, although growing abundantly almost in the same mass and having the same fruiting season.

I am inclined to think that not enough emphasis is given to the fact that the lower plant forms do not have a continuous period of growth, either vegetative or reproductive. In other words, the normal period for either activity is continuous for only a few weeks or months at most; it remains a problem of research to show how inclusively this generalization applies to the freshwater algae. For Spirogyra the observations reported in this paper seem to offer overwhelming evidence in support of the view, for this region at least, that it is not a perennial plant. I have only a single exception to this conclusion and will speak of it later. A few of the species studied appeared more or less abundantly in the fall; in this connection *S. Hantzschii* furnishes a specific example. In a majority of the forty localities kept under observation during 1905–6, several forms of algae succeeded one another in maximum abundance in the course of a year. In only four of the forty places was any trace of Spirogyra found in the fall where it had been in a state of conjugation in the spring. The manner in which different species appeared, matured, and conjugated was for most of the forms quite distinct and constant for the several localities. Following the fruiting season the disappearance of the plant took place sometimes suddenly and sometimes gradually.

It is a well-known fact that vegetative material is very difficult to identify; the same might as well be said of conjugating material. For this reason it is difficult to follow any given species with certainty;

where several closely allied species are associated, this is practically impossible. Fortunately this did not occur except in a few places. However uncertain and unreliable may be one's observations and conclusions relative to a given species during its period of vegetative growth, it is possible to determine with some certainty whether or not the different species of Spirogyra have any definite or fixed periods at which they conjugate, or whether this phenomenon takes place only under certain conditions of environment. In all cases notes were taken at each visit to a pond, and the determination of the species left until the fruiting season; then by going back to my notebook, the life-history could be worked out with some certainty. Leaving out of account uncertain conditions such as the vegetative activities, and placing special importance on the period at which conjugation takes place, it is possible to conclude that one of the two important phenomena (vegetative and reproductive activities) in the life-history of this alga appears periodically, not due exclusively to seasonal conditions nor to environment.

No one can say with absolute certainty whether the natural forces that produce conjugation are internal or external. It is a fact, however, that whenever a condition was present, in any part of a mass, which was able to initiate and control reproductive activity, there was at the same time and place either the same or some other condition which brought about the destruction of all vegetative filaments. In this study no exception was found to this rule, whether under laboratory or under natural environment.

Up to the time when conjugation was abundant in ponds, brooks, and ditches, I still had over 300 aquaria in the laboratory. A small percentage of them contained fruiting Spirogyra. The time of fruiting for any given species began about one week earlier and lasted about one week longer in the laboratory than that of the field. The disappearance of the vegetative filaments was also more gradual. It was not difficult to keep aquaria early in the year, but after the middle of May they began to decline and were kept only with increasing care until mid-summer, when out of 700 only one remained.

As to the different sizes of aquaria, it ought to be said that some were ordinary test-tubes; some contained 25–30 liters; and the majority ranged from one to ten liters. The results were not constant for either the large or small sizes, although all sizes were usually arranged at the same time. In dozens of test-tubes two-thirds full of water or culture media Spirogyra kept well two to three months. On the average, however, aquaria of four to ten liters were most satisfactory. In three large aquaria of about forty liters each no successful cultures were made, although frequently attempted.

An attempt was repeatedly made to grow Spirogyra in some of the larger aquaria after a species had died in it and without renewing the culture media. In every instance where this was tried the plant died down in a few days, showing that the solution contained a toxin injurious to Spirogyra. It is left as an open question whether a mass of Spirogyra in nature dies from the accumulation of this same destructive element.

Aside from the twelve species herein described, there was still another which has been kept under observation since early in the fall of 1905. It is a large form and was found growing in rather large bright-green patches in the running water of three different brooks one to three miles apart. When first found, a few aquaria were started, one of which has remained to the present time without any indication of decline. This is an ordinary aquarium of about 10 liters; it is kept well covered and for that reason very little evaporation takes place. The main algal associate is Oedogonium, and a few brown and green hydra have lived in the aquarium from the beginning. This jar is the one exception to the 700 aquaria that died down during the season of 1906. In concluding, I wish to call attention to the fact that no trace of a conjugating filament has been found in this aquarium; and furthermore, that none was found at any of the three brooks mentioned, although in one case the plant was very abundant. It is also remarkable that there has not been a time from the first when vegetative specimens of this species could not be obtained.

In addition it ought to be said that this study was continued during the following year (1906–7), in the same locality, under about the same conditions and methods of study. This second year's observations and experiments did not vary enough from those of the previous year to warrant any change in the conclusions above given.

Summary

1. Few of those who have published papers on the genus Spirogyra have given any notes on the subject of periodicity.

2. Out of 700 aquaria it was found that the best way to arrange a culture was to place some sterilized earth in the bottom, add some dead leaves or dead grass, allow to settle well, then add a small amount of Spirogyra, and place at first in a window not exposed to direct sunlight.

3. Of 300 aquaria in the laboratory at the time when Spirogyra was fruiting most abundantly under natural conditions, there were about 5 per cent. which contained conjugating material. The time corresponded with that of the field.

4. Leaving out of account the number of species which may have been collected in the vegetating condition and for that reason doubtful of identification, there were at least thirteen different species collected, of which twelve fruited more or less abundantly.

5. Ten of the thirteen species passed their period of maximum abundance in May, one in August, and one in October. A few doubtful fruiting filaments of *S. Hantzschii* were found a second time in August. The only reliable example of a second fruiting period found was *S. dubia*, which fruited in May, and again in small patches, but relatively abundant, during the latter part of July.

6. When field-work was first begun, material was collected and then brought to the laboratory for examination. This method was by no means satisfactory and for that reason was discarded. All the later collections were examined on the spot with a microscope.

7. The period of maximum abundance corresponds in every case with the period of maximum conjugation. The decline of one was always accompanied by that of the other.

8. After conjugation had ceased the fruiting filaments disappeared more or less gradually. The vegetative filaments also disappeared, and at the same time as those containing zygospores.

9. In the laboratory no Spirogyra was found fruiting at the surface but always near the substratum. In the field the reverse was true. *S. orthospira* and *S. Hantzschii*, however, were prominent exceptions.

10. Of the thirteen species one has not been found in a state of conjugation. It has been kept under observation, in excellent con-

dition, both in the laboratory and in the field, since October, 1905, but no trace of fruiting material has been found.

11. Notes taken in the field and supplemented by those in the laboratory offer overwhelming evidence in support of the view that the phenomenon of conjugation results not so much from external as from internal conditions.

12. The writer therefore concludes that Spirogyra has definite periods of growth and activity.

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ON THE POLLEN OF *MICROCACHRYS TETRAGONA*

ROBERT BOYD THOMSON

(WITH PLATES I AND II)

"*Microcachrys tetragona* occurs only on the highest summits of the Western Range and Mount Lapeyrouse in Tasmania. It was introduced to the Royal Gardens at Kew about the year 1857 by Mr. WILLIAM ARCHER, on whose property it grew. Although of great interest in a botanical sense, its only value as a garden plant is for conservatory decoration, for which the elegant habit it can be made to assume under pot culture, its neat foliage, and bright-red fruits render it highly suitable."[1] The specimens for this work were obtained through the kindness of the present director of Kew Gardens, Colonel PRAIN, whose courtesy and that of the staff is much appreciated by the writer.

The general features of the fruiting branches of microsporangiate and megasporangiate plants are indicated in *pl. I*. The cones are borne terminally and their sporophylls are spirally arranged, in contrast to the opposite and slightly concrescent vegetative leaves (*pl. I*, and *pl. II*, *fig. 1*, the branch to the left).

The microsporophylls bear two somewhat spherical, pendant sporangia (*fig. 2*), whose form and structure, after the discharge of the pollen, is indicated in *figs. 3* and *4*. The terminal scale of the sporophyll is broadly triangular in outline (*fig. 2*), very much extended dorsally (*fig. 3*), but not, or scarcely at all, in the ventral direction. The inner layers of the wall are much collapsed at the stage indicated, but the epidermis retains a very definite structure on account of its peculiar thickened bands. These are shown in transverse and in longitudinal section in *figs. 5a* and *5b*.

In *fig. 4* some linear and branched structures are apparent in and around the sporangia. These are the hyphae of a fungus, and to their presence the retention of many of the pollen grains in the dehisced sporangia of my material is due. The hyphae are often in intimate association with the pollen, they frequently branch, and the branches form contact with the grains. This pollen is no different from the less abundant found in uninfected sporangia.

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[1] KENT, ADOLPHUS H., Veitch's manual of Coniferae 161. 1900. The references to the discovery of this form and its description are given here.

The pollen of Microcachrys (*fig. 8*) is small as compared with that of Saxegothaea (*fig. 9*), Podocarpus (*fig. 10*), or Pinus (*fig. 11*), all these figures being the same magnification for the purpose of comparison. The grains vary considerably in size, a feature which my material of Saxegothaea also shows. They are winged, though in some instances I have thought that no wings were present, but more material was needed to determine this point than was at my disposal. The wings arise in the ordinary way by a separation of the exine from the intine. In longitudinal section the grains usually show two rather poorly developed wings (see various grains in *fig. 6*), and in following the series these two are often all that one can be certain of. In gross material, however, three wings are readily apparent (*fig. 8*).[2] In transverse sections, also, which pass through the ventral part of the grain, the three-winged condition is clearly seen (see middle of *fig. 6*). In some cases one of the wings is very small (*fig. 6*, grain in upper part of the field). The lowest grain in *fig. 6* shows the presence of four wings (the central one very dark). Some four-winged grains have one pair of wings much smaller than the other. Exceptionally, five and six-winged grains are found. A student, Mr. W. P. Thompson, kindly made a careful determination of the number of wings in gross material from several cones, rolling the grains in fluid under the cover glass. He found that of sixty-four grains, fifty were three-winged, three of these having one very small wing; nine were four-winged; two had five, and three had six wings. The pollen studied was in the mature condition and the wings must have been fully developed. *Fig. 7* shows the greatest expansion of the wings that I have observed. They usually do not extend laterally beyond the body of the grain (*fig. 8*, also some grains in *fig. 6*). They project, however, beyond the body of the grain ventrally, though not to such a degree in either direction as do those of Podocarpus (*fig. 10*) or Pinus (*fig. 11*). A small amount of material from the apex of one of the cones showed another feature. When the pollen grain has a five-celled gametophyte, the wings are very small, not much larger than they are in Pinus when its pollen is still in the tetrad condition. The wings of Microcachrys arising thus late ontogenetically give indication of their recent acquirement.

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[2] I studied the grains in section first, and this led me to misinterpret the number of the wings, as stated in Bot. Gazette **46**:465, 466. 1908.

With regard to the microgametophyte, I find that in the mature condition of the pollen four prothallial cells are often present, though three are more usual. When three only are present, it is the second prothallial cell that has divided (*fig. 7*). The first and second prothallial cells have walls which turn blue with chlor-iodide of zinc. No further cellulose walls were demonstrated. *Fig. 7*, in addition to the prothallial cells, shows a lateral derivative of the body cell and the tube nucleus. The gametophytic structure thus conforms to that which recent investigators have shown characterizes the related forms. Perhaps it is not out of place here to give credit to THIBOUT,[3] the first person, so far as the writer knows, to describe and figure a multicellular gametophyte in the Podocarpeae.

NORÉN in his recent work on Saxegothaea[4] has emphasized the relationship of this form to the Araucarieae. He finds that, in addition to the supernumerary prothallial cells, there is a curious reminiscence of this group in the mode of pollination, the pollen sometimes being deposited in the cavity around the ovule and growing over the tissue into the micropyle, a condition which so far as can be judged is essentially similar to that which I have found in Agathis. He also calls attention to the wingless condition of the pollen in both Saxegothaea and the Araucarieae.

With the present contribution our knowledge of the occurrence of excess prothallial tissue in all genera of the Podocarpeae is complete. The winging of the grain in Microcachrys is of varied and indefinite character, late in development, and undoubtedly of primitive type, the form occupying in this respect an intermediate position between Saxegothaea on the one hand and Dacrydium and Podocarpus on the other. This is the more evident from the presence of three wings in some species of Podocarpus. THIBOUT describes the

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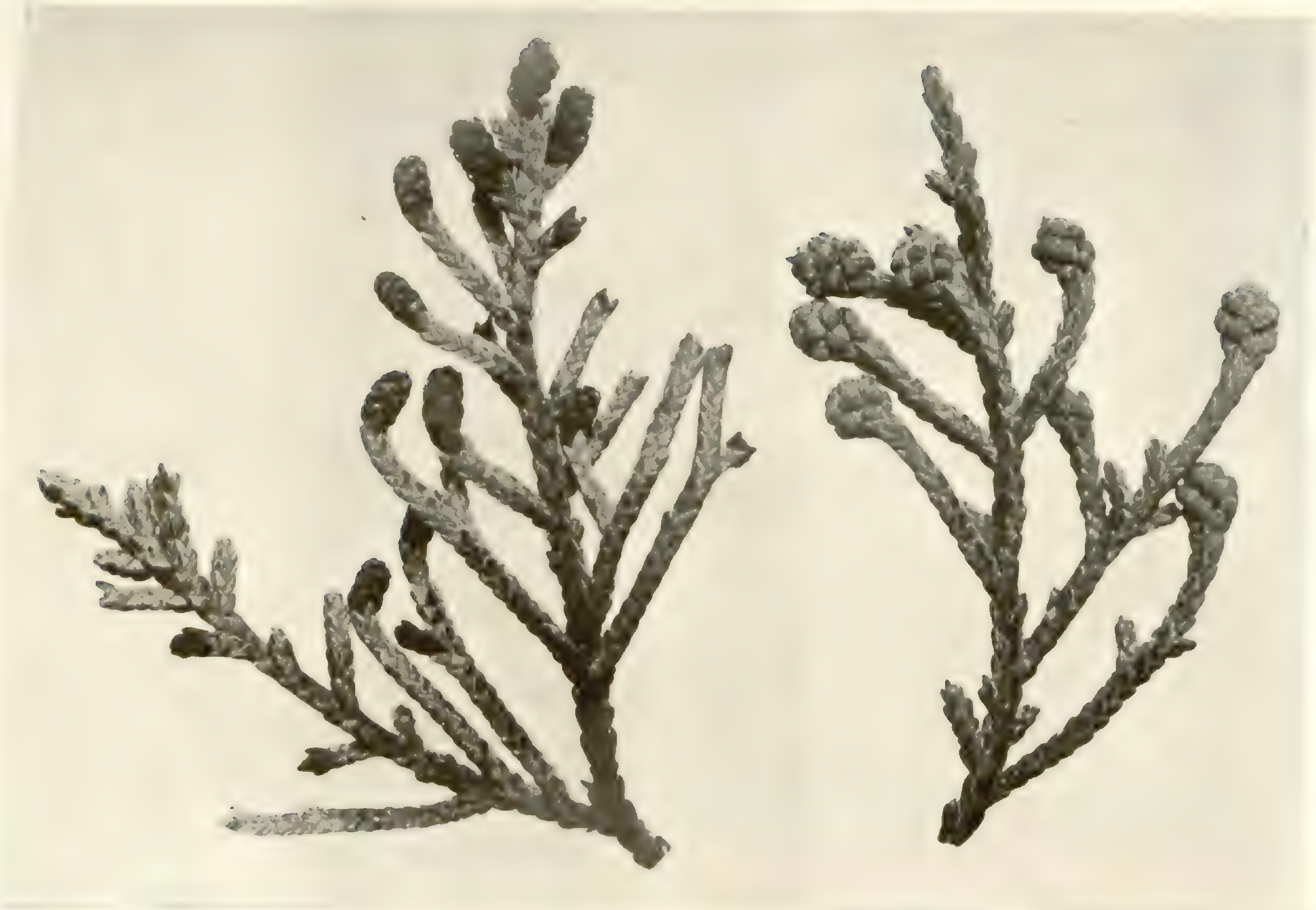
[3] THIBOUT, E., Recherches sur l'appareil mâle des gymnospermes. pp. 265. *pls. 16*. Lille. 1896. See *pl. 14, figs. 8* and *9*, of *Podocarpus polystachya*.

[4] NORÉN, C. O., Zur Kenntnis der Entwicklung von *Saxegothaea conspicua* Lindl. Svensk. Bot. Tidskr. **2**:101–122. *pls. 7–9*. 1908.



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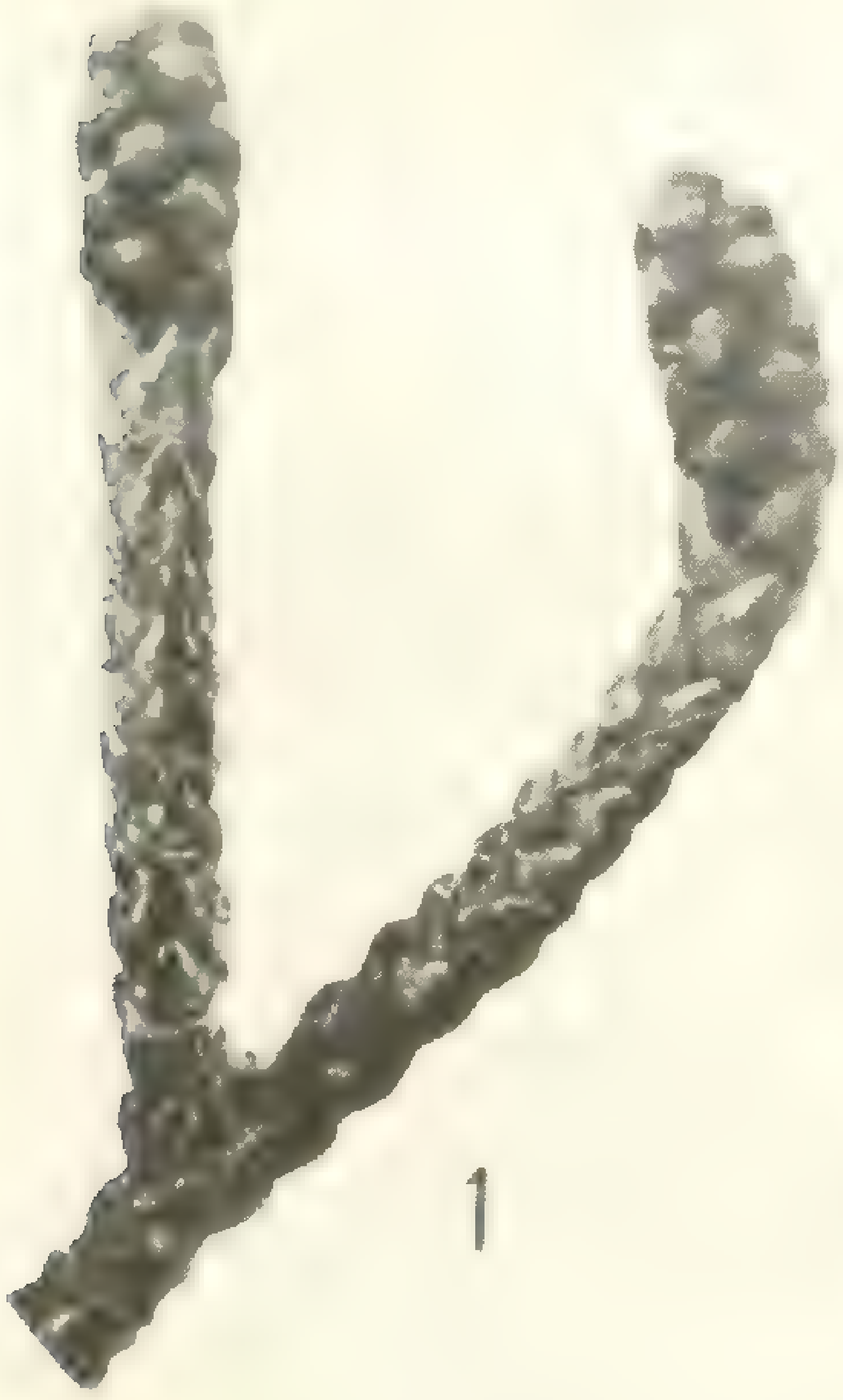
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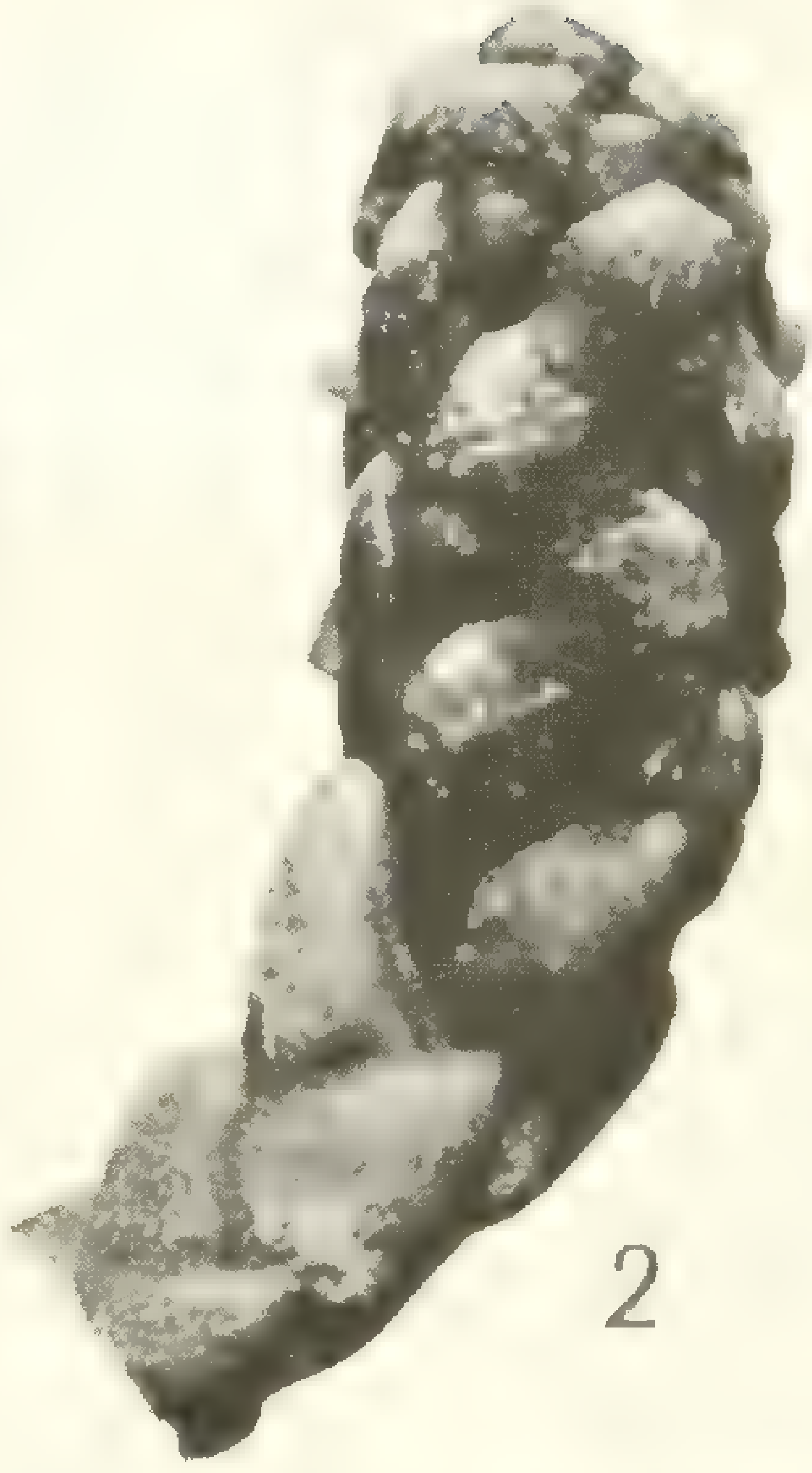
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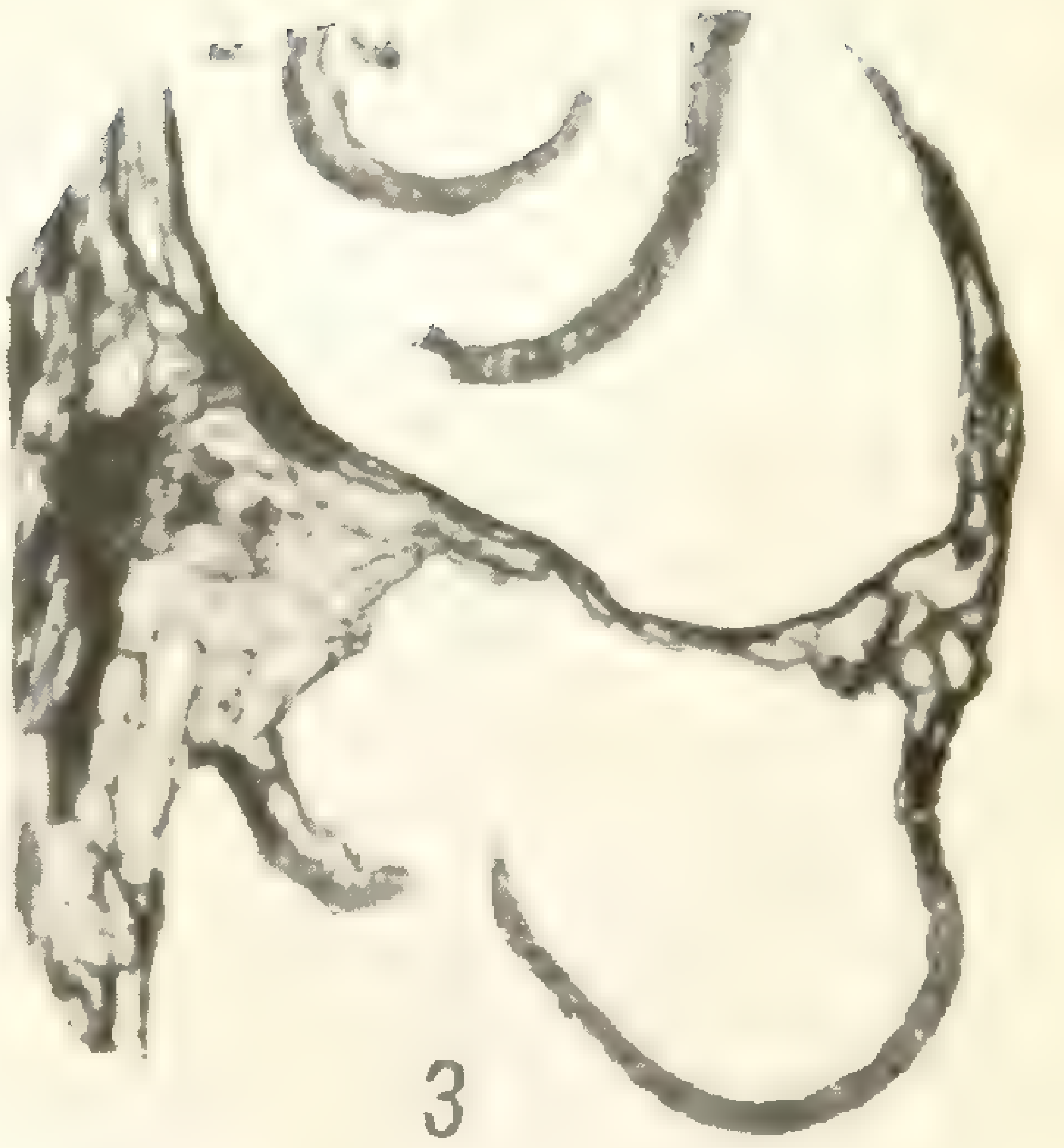
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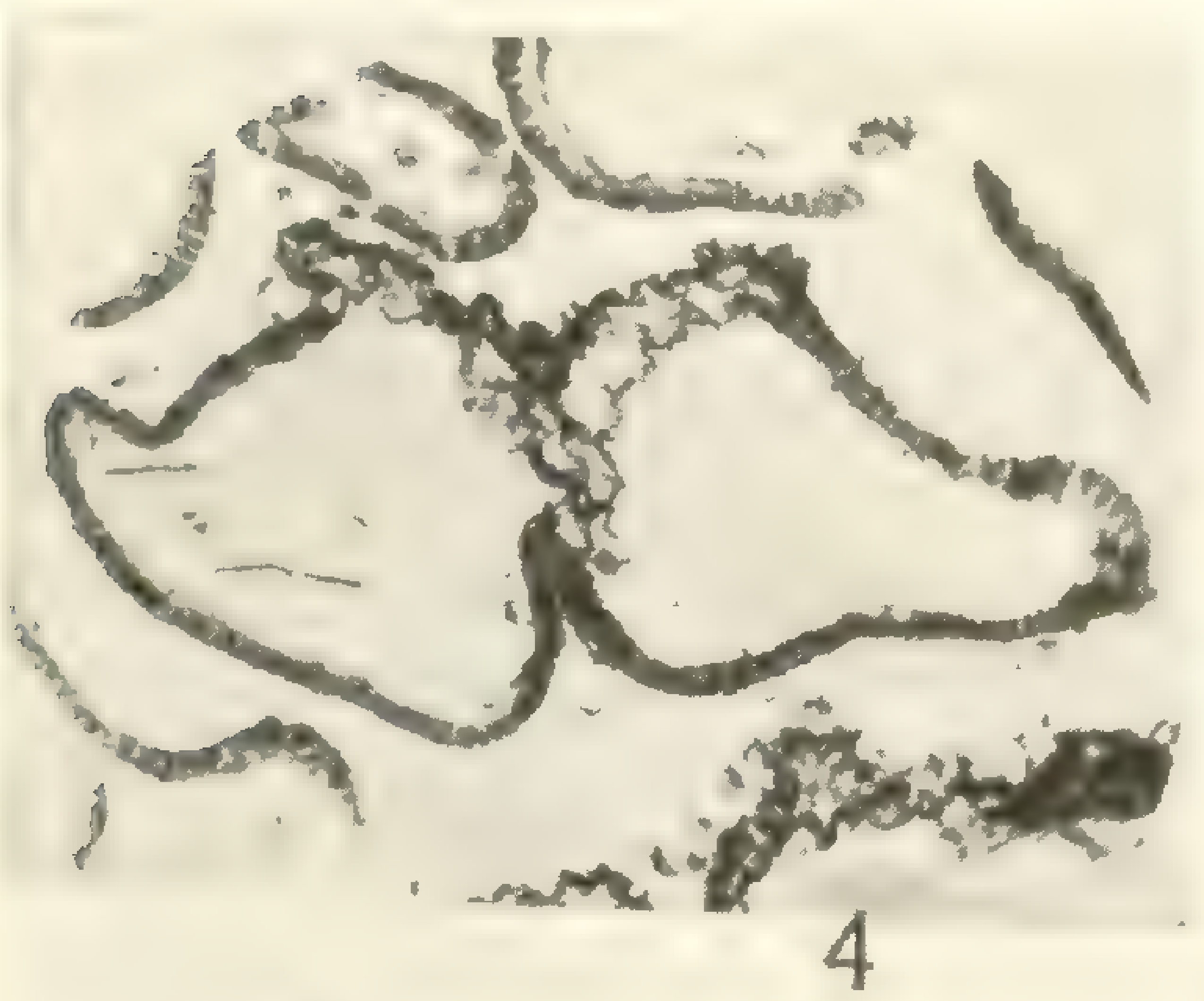
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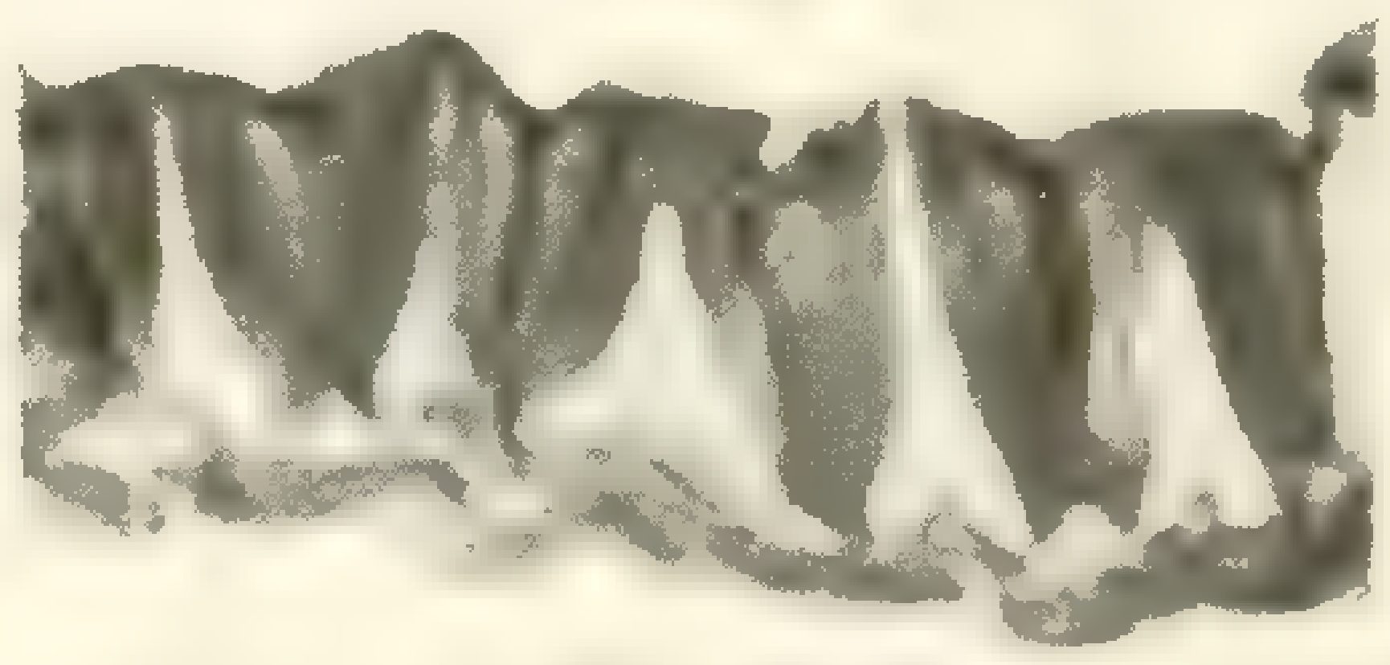
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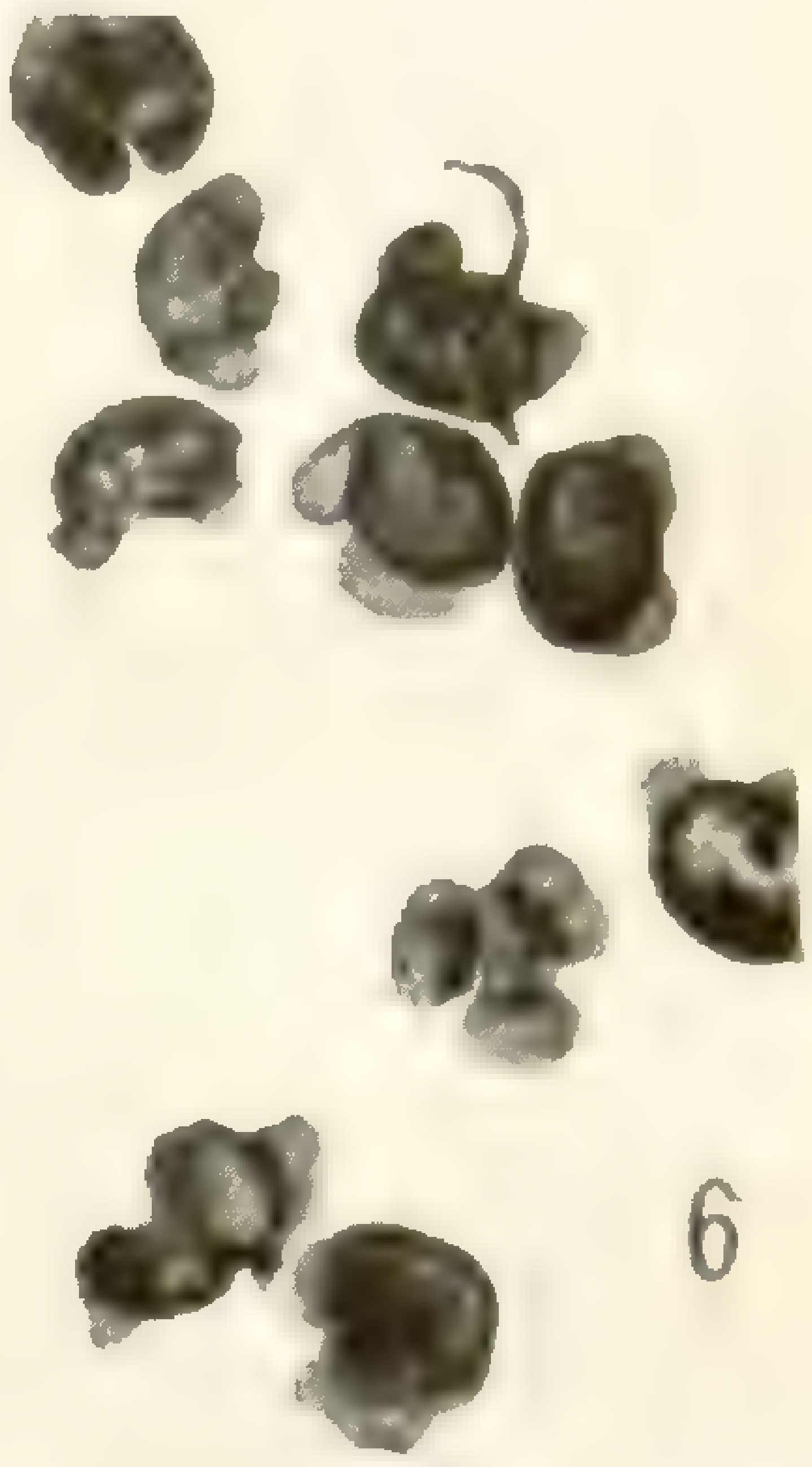
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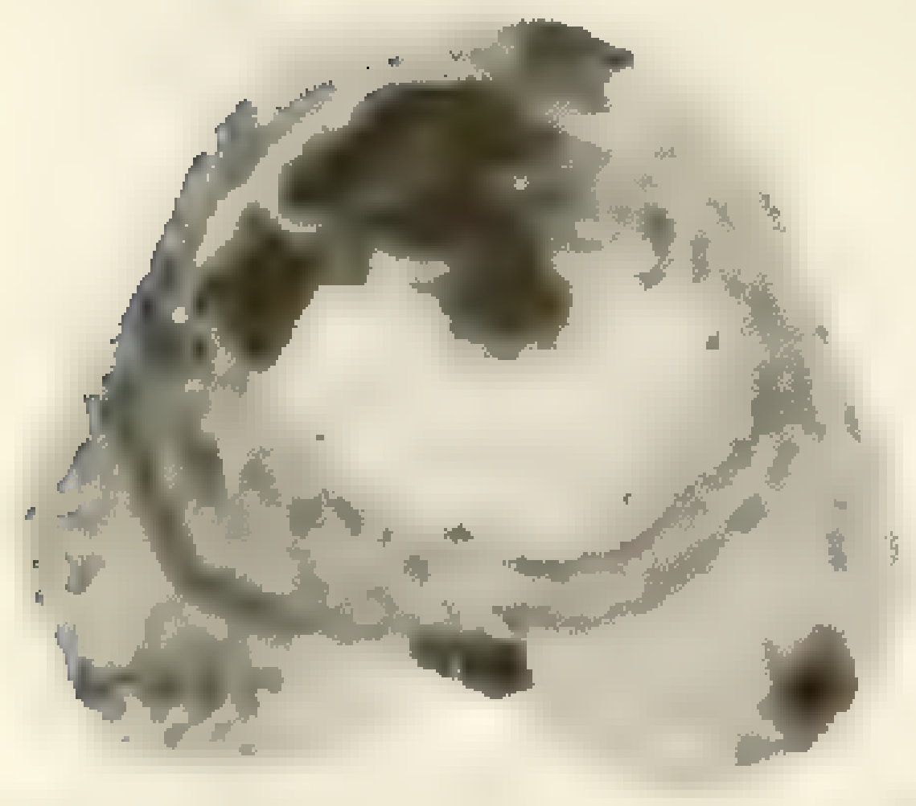
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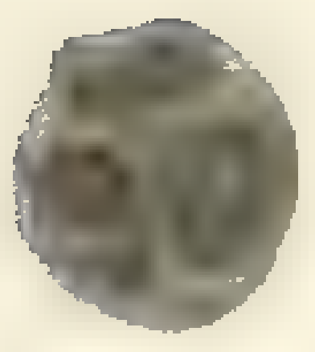
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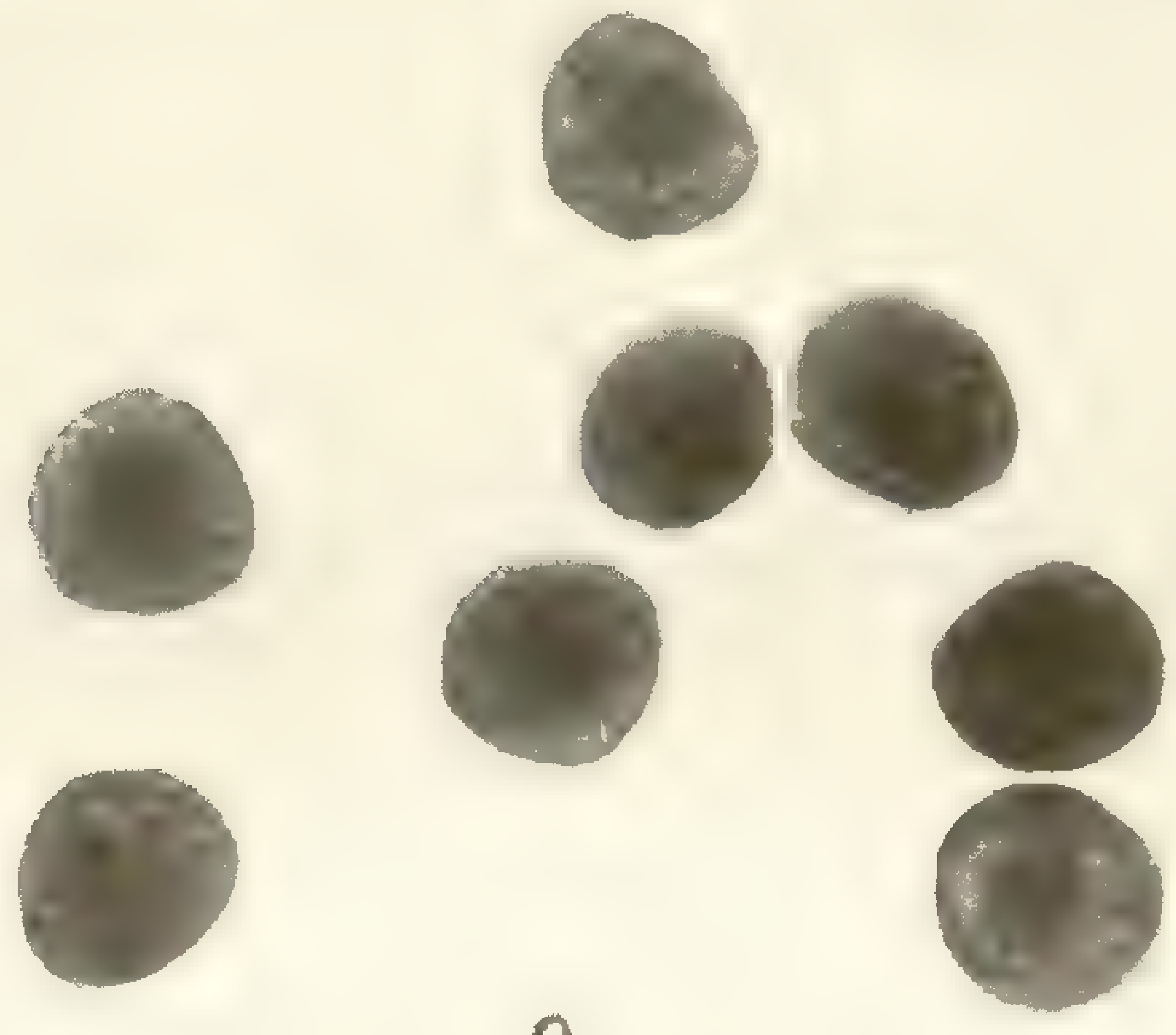
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10 *a*

10 *b*

10 *c*

11

12

THOMSON on MICROCACHRYS

pollen of *P. dacrydioides* as having normally three wings (*op. cit.*, *pl. 14*, *figs. 10*, *11*). I have found three wings present exceptionally in the usually two-winged *P. ferruginea* (*fig. 12*). Unfortunately, no data nor material of the more probable genus Dacrydium were available.

The bi-winged condition of the pollen on the pines and podocarps has often been referred to as an indication of affinity between the groups. This view has no longer support, since the winging of the grain has arisen in the Podocarpeae within the group itself, and so is distinct from that of the pines. In a further contribution on the character of the megasporophyll of Saxegothaea and Microcachrys, the writer hopes to show the essential difference of this structure in the two great phyla of the conifers.

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EXPLANATION OF PLATES I AND II

PLATE I

Twigs from staminate and ovulate plants. ×2.25.

PLATE II

FIG. 1.—Branch with microsporangiate cones. ×4.

FIG. 2.—One of the same enlarged; the sporangia can be seen in pairs beneath the terminal scale of the sporophyll. ×9.

FIG. 3.—A microsporophyll in longitudinal section, to one side of the axis.

FIG. 4.—Same in transverse section; the linear structures in the sporangium are the hyphae of a fungus shown in contact with pollen grains in *fig. 6*.

FIG. 5*a*.—The wall of the microsporangium in tangential section.

FIG. 5*b*.—The same in transverse section.

FIG. 6.—A field of sectioned pollen grains; below is one with four wings; above it one with three wings cut transversely and a small part of the body uniting these; various other aspects of the wings.

FIG. 7.—The microgametophyte.

FIGS. 8–11.—Pollen grains at same magnification: *fig. 8*, Microcachrys, from below; *fig. 9*, Saxegothaea; *fig. 10*, *Podocarpus ferruginea* (*a* and *b* two latera views at right angles; *c*, dorsal view); *fig. 11*, *Pinus resinosa*.

FIG. 12.—A three-winged grain of *Podocarpus ferruginea*.

A VEGETATIVE MUTANT, AND THE PRINCIPLE OF HOMOEOSIS IN PLANTS

CONTRIBUTIONS FROM THE AMES BOTANICAL LABORATORY, NO. 9

ROBERT GREENLEAF LEAVITT

(WITH NINETEEN FIGURES)

When viewed in their relations to morphogenetic and broader evolutional problems (as distinguished from narrower phylogenetic, or genealogic, problems) numerous facts of teratology—a descriptive cult without unifying principles, heretofore pursued chiefly by the vaguely curious, and lending itself discreditably with equal readiness to either side of many a morphological discussion in the past—manifest a special and high value. The production of form from formlessness in the egg-derived individual, the multiplication of parts and the orderly creation of diversity among them, is an actual evolution, of which anyone may ascertain the facts, but of which no one has dissipated the mystery in any significant measure. This micro-evolution forms an integral part of the grand evolution problem and lies at the base of it, so that we shall have to understand the minor process before we can thoroughly comprehend the more general one. Morphogenetics, therefore, is a field in which the evolutionists must work. The development, or morphogenesis, of a single individual—if it be such a case as may improve our insight into the nature of the ontogenetic process micromechanically considered—may be of as great interest in the eyes of the evolutionist as the origin of a new race or the fate of an old one.

It is this relation, to the central rather than the peripheral problems of evolution, which has led me to carry out certain observations upon abnormalities in plants. Yet I shall try to make clear, also, the bearing which some of the observed individual variations have upon types of racial variation. In this connection some facts of normal, i. e., established, morphology will be noticed. The main principle under discussion seems to deserve a place, though a minor one, in any complete account of the evolution of species.

The present paper is sequel to a casual observation made several years ago, when as I was passing near a horsechestnut tree in the autumn I noticed, upon a depending branch, a leaf which had lost several of its leaflets. I found that the palmately compounded leaves of this species fall to pieces as they are cast off by the tree, or even before this event. The leaflets are removed as if by a clean cut; and sometimes the petiole, quite devoid of blades, is left standing alone upon the stem.

This complete dismemberment seemed to me a curious thing. Abscission at the base of the petiole is not a simple decay, but is, as everyone knows, a somewhat complicated process, wherein there is formed across the leaf-stalk, through suitable cell divisions, a plate or layer of cells, by the disintegration of which the leaf is ultimately allowed to fall away. The cell walls of the scar-surface become suberized, so that the wound is sealed against the loss of water. Leaf-abjection is thus a complex adaptive process.

The question arose, Why should the abscission proper to the petiole-foot be repeated in all of its details at the bases of the petiolules?—for I ascertained that the process is carried out in full at these points in this species. Of what use to the tree is it that the frame of the leaf, now emptied of its valuable contents which have been withdrawn into the stem, should be carefully disarticulated? I have never been able to imagine any utility nor have those to whom I have propounded the riddle suggested any. I believe that in fact the habit is neutral in the tree's economy.

If this is so, the evolution of absciss-layers in petiolules cannot be referred to natural selection. For in the plan of evolution by the accumulation of variations under the guidance of natural selection, developing organs must pay their way as they go.

An explanation of the presence of the useless structures occurred to me. It seemed probable that the absciss-layer perfected in the natural course of evolution at the foot of the leaf-stalk had, subsequently to the compounding of the blade in this species, been transferred, so to speak, to the bases of the petiolules. The disarticulations of the leaflets seemed to be a series of ecologically meaningless echoes of the primal, useful disarticulation at the junction of stem and petiole.

The horsechestnut is not peculiar in this respect, and further considerations, with regard to compound leaves generally, have confirmed in my own mind my first understanding of the matter. Disarticulation of the leaflets seems to be universal in deciduous-leaved species. It occurs in many families separated in a natural system by entire-leaved groups, as in Juglandaceae, Berberidaceae, Anonaceae, Rosaceae, Rutaceae, Sapindaceae, Vitaceae, Oleaceae, Bignoniaceae, Caprifoliaceae. That is, it must have arisen in evolution many times independently. There must, then, be some wide underlying principle capable of bringing the disarticulation in question to light, wherever compounding of the blade establishes the conditions for its operation. This principle seems, as has been argued above, not to be natural selection. There is, however, in plants a recognizable principle of morphic translocation, mobility of characters, or *homoeosis* (BATESON), to which the phenomenon may very well be referred.[1] The conditions favorable to its operation in this case are very obvious, since the structural relations at the junction of the petiole and stem are imitated at the junction of petiolule and petiole (or rhachis).

The Pierson fern

Recently evidence corroborating the above interpretation has come to hand in a case where advance in complexity has been all but observed. In the title I have alluded to it as a case of mutation; but perhaps I am using the word somewhat loosely, if the DeVriesian sense is to be insisted upon. The plant is the Pierson fern, now well known to horticulturalists and to the public generally. The metamorphosis of the Boston fern, to which the Pierson owes its origin, seems not to have been hitherto described as a homoeotic transformation; yet such it is.

The first plant of the variety was found while it was still small, among vegetatively propagating Boston ferns in the greenhouses of Mr. F. R. PIERSON, the well-known horticulturalist of Tarrytown-on-Hudson, N. Y., in 1900.[2] While it was not a "pedigreed" plant, its derivation is patent, for when its descendants are grown under poor conditions, they generally revert temporarily, in a part of their fronds at least, into the primitive state, which is seen to be that of the Boston fern. This constitutes highly desirable proof of parentage. Whether the sudden alteration of character took place in a spore, or in a bud from a runner, is not surely known. Nevertheless the circumstances leave little doubt on this head; for the Boston fern, while richly stoloniferous, is almost universally sterile. Mr. PIERSON believes the original individual to have been a bud-sport. The young plant caught the eye of a gardener, who brought it to the notice of Mr. PIERSON, and it was set aside so that its development might be followed. All Pierson ferns and numerous varieties have descended from this individual.

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[1] My first paper on this topic, entitled "On translocation of characters in plants," appeared in Rhodora 7:14–19, 21–31. 1905. When it was written I did not know that BATESON had briefly treated the same subject in relation to variation of animals and had devised the name homoeosis. I find his term applicable to the present purpose and more convenient to use than my own expression.

[2] Mr. F. R. PIERSON, in a letter to the writer.

In this case we may say that the transformation, which affects the leaves of the fern and consists not in the introduction of altogether novel outlines or proportions, but rather in the relocation of forms already in existence, has taken place under observation. A single individual has been noted to emerge from the common mass—under cultivation as an isolated colony—with very markedly altered characters. New features have not been slowly developed through several generations, but have appeared suddenly.

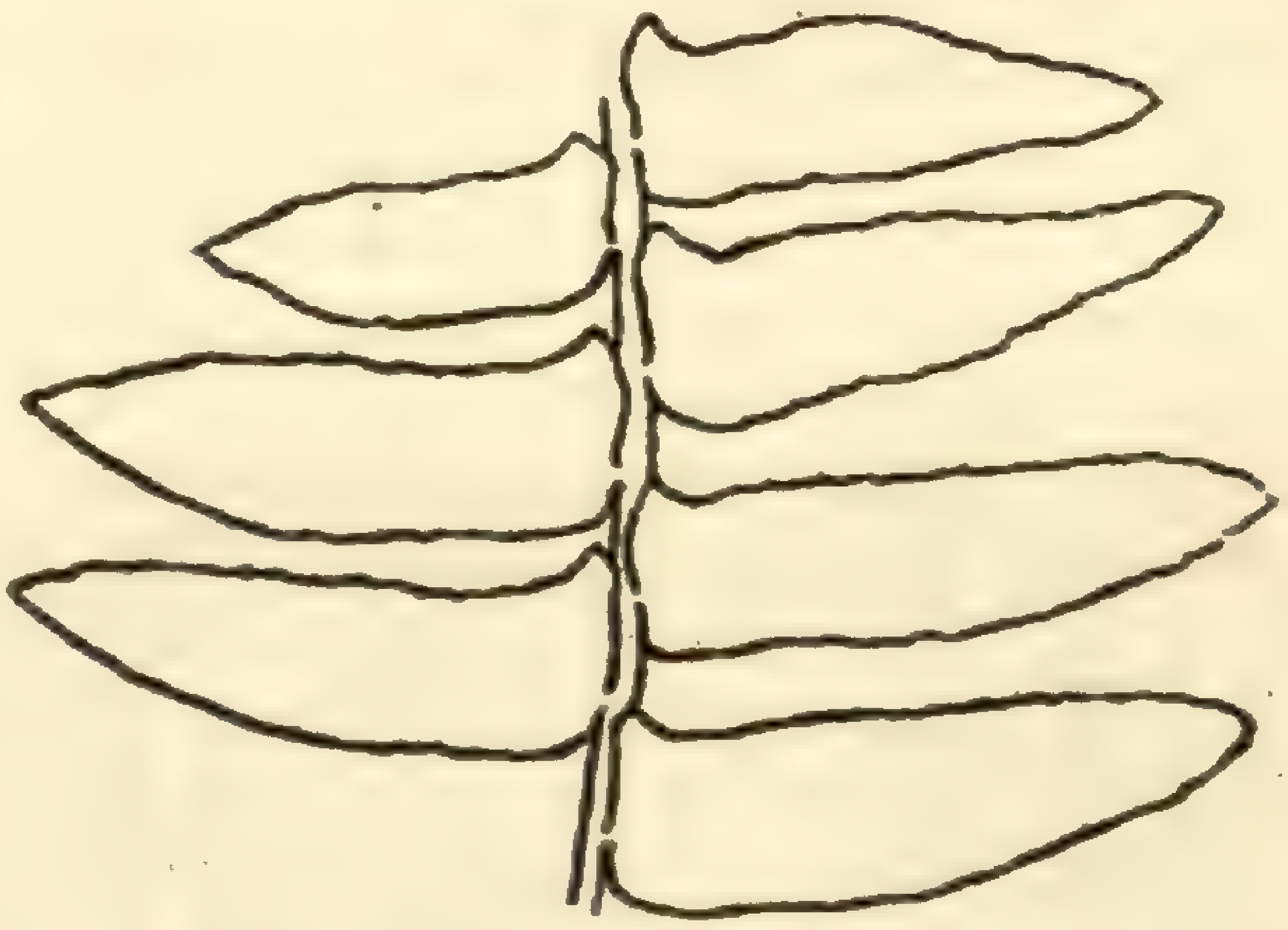
FIG. 1.—Pinna of Boston fern.

The Boston fern has simply pinnate fronds. The pinnae are entire, serrulate-margined, oblong, and usually bluntly toothed or auriculate on the upper margin at base (*fig. 1*). In the new plant, the pinnae have become divided,[3] and at the same time elongated—often much elongated. Their divisions, the pinnules, are oblong and, when fully developed, toothed or auriculate on the upper margin at base (*fig. 2*). The pinnules, in fact, are very good copies of the

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[3] When the new form is fully expressed. The division may affect only part of each pinna.

original pinnae; and if we lay a well-developed pinna of the Pierson fern by the side of a small frond of the Boston fern, we shall be struck with the fact that they are almost identical. In short, the pinnae of the new variety are transformed from the original condition in such a way that the plan of the whole frond of the Boston fern is now seen in the primary segments of the Pierson frond.

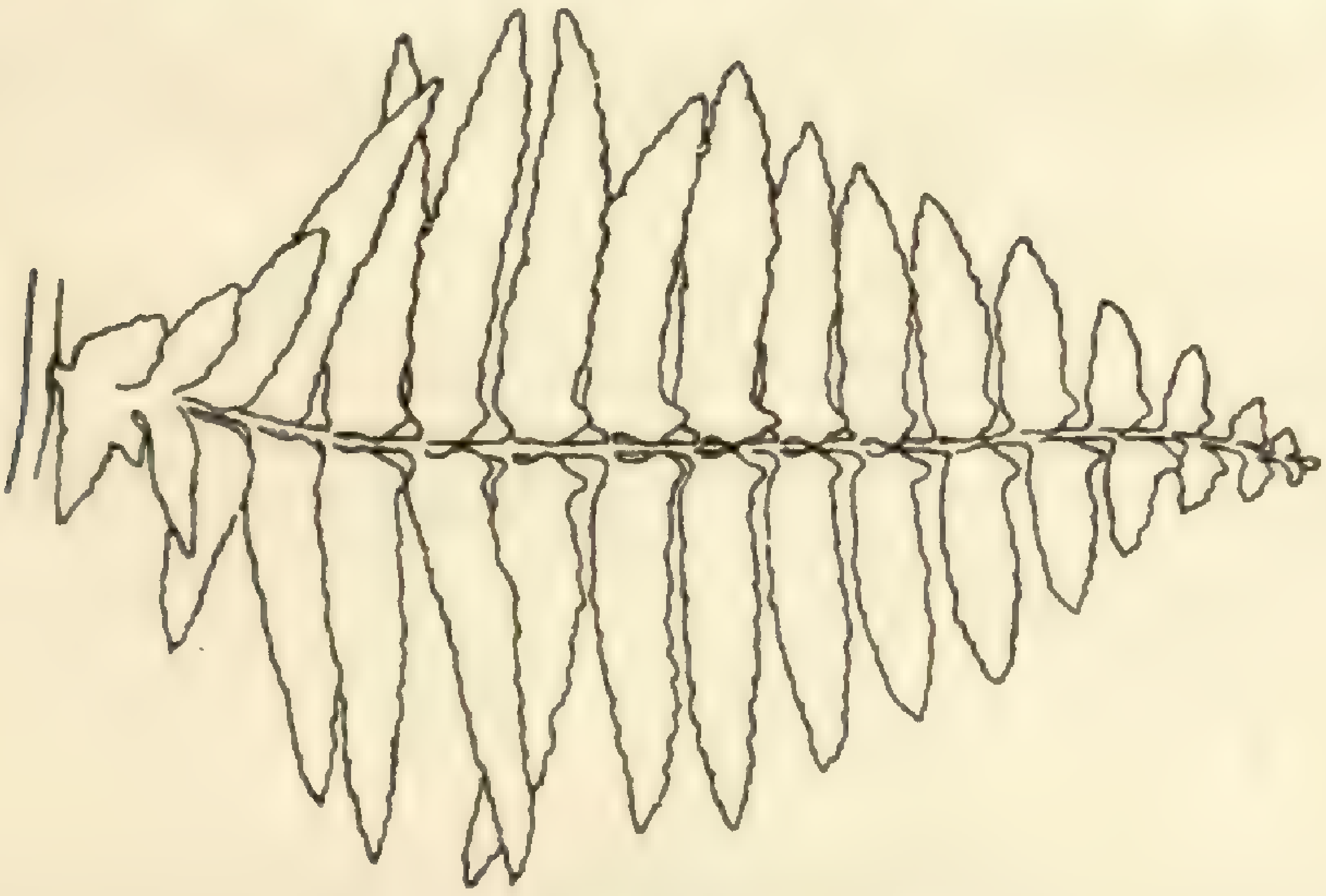

FIG. 2.—Pinna of Pierson fern.

The completeness of the imitation may be indicated still further:

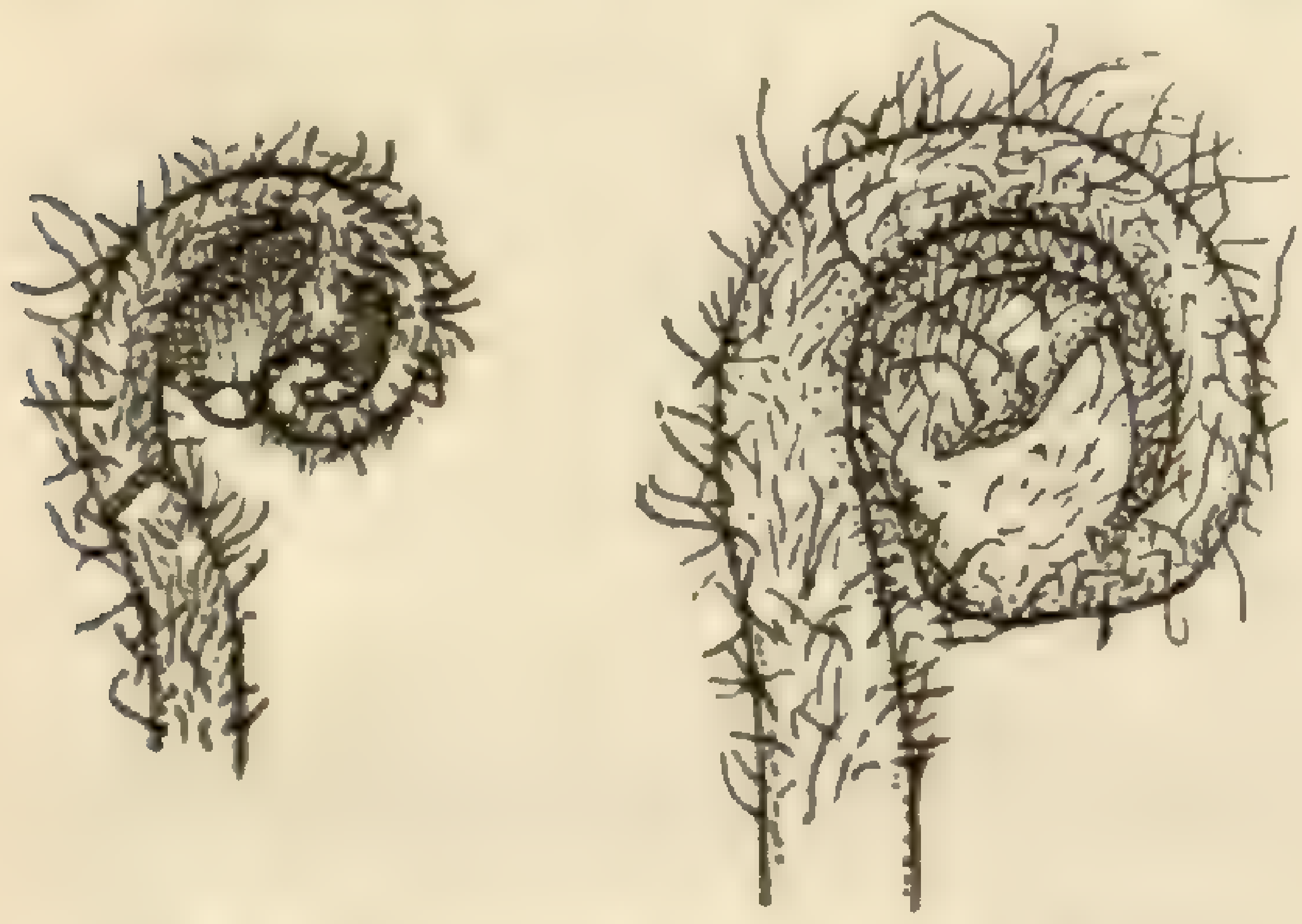

FIG. 3.—Growing apex of pinna of Pierson fern (left) and Boston fern (right).

1. The pinnae are elongated, the growth being less strictly determinate than that of the original pinnae, and more like that of the frond.

2. The apical growth of the pinnae is now circinnate, as shown in *fig. 3*, after the fashion of the original frond. The pinnae of the Boston fern on the other hand, while lapped together in the young state at the summit of the developing frond, are not in the least circinnate.

3. The blades of the pinnae are divided.

4. The outline of the pinnules is like that of the original pinnae.

5. Finally, the peculiarity of the original form, that its pinnae in age become disarticulated by the development of an absciss-layer,

and ultimately fall off after several layers of brown tissue have been developed on the scar surface-to-be, is now shown by the pinnules of the Pierson fern. The pinnules of the latter are discovered to be deciduous, and a minute investigation shows that deciduity is secured by the development of an absciss-layer at the base of the pinnule, with the formation of brown scar-tissue. Thus the translocation of the structures concerned in disarticulation of leaflets is in this case an ascertained occurrence: these structures have passed at once and unaltered from the bases of the pinnae to the bases of the pinnules.

The beautifully soft and luxuriant aspect of such ferns as the Whitman[4] is due to the fact that each frond is in effect made up of many small fronds. In this last-named variety, and in some others, as Pierson's *elegantissima* and *superbissima*, homoeosis has gone one step farther than in the Pierson, so that we find a thrice-compounded leaf (*fig. 4*), and the segments of the third order have the frondlike character—even to the circinnate apical growth.

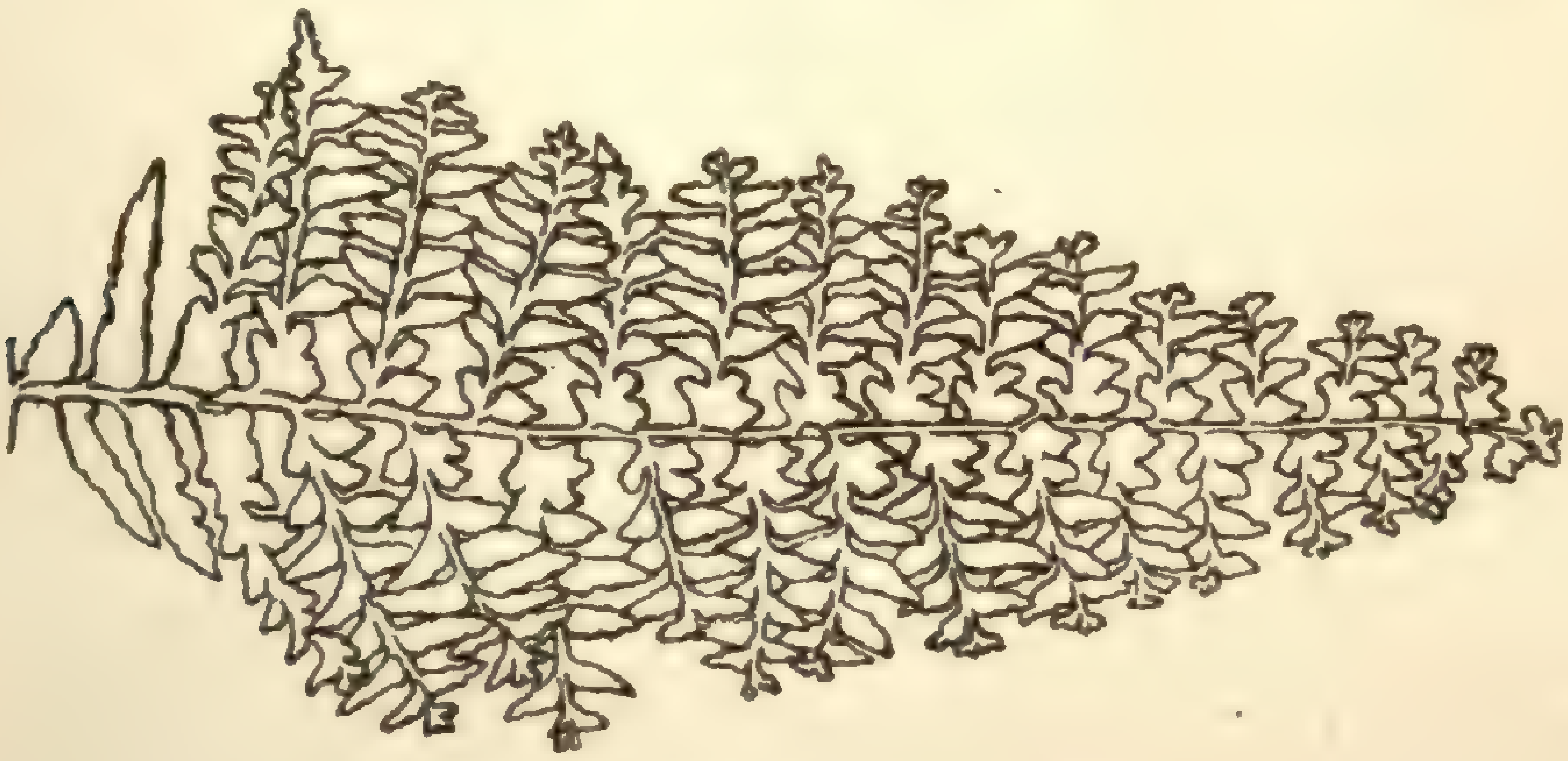

FIG. 4.—Pinna of Whitman fern.

To return to the matter of normal casting of leaflets, with which we began. The fact that in an instance now before us positive evidence of the translocation of absciss-layers, etc., from one part of the leaf to another has been secured, strongly corroborates the inference already made on more speculative grounds, that leaflet-abjection in general is to be understood as an imitative or repetitive phenomenon.

[4] The Whitman fern originated in the greenhouse of H. H. BARROWS & SON, Whitman, Mass., in 1904, as a bud-sport, upon a runner of the Barrows fern (itself a sport from the Pierson).—Letter from H. H. BARROWS & SON to the writer.

The principle of homoeosis

But whether or not the transference of absciss-layer from leaf to leaflets in this fern verifies in any material degree the idea of a translocational origin for leaflet-abjection, it alone, were there no other available demonstration, would suffice to establish the important truth, that a character perfected in the course of evolution under one relation in the plant body may make its appearance suddenly under another relation and in a region of the body to which it is not native. Here is a principle of wide import in morphogenesis, and not without bearing—as has just been shown—upon some of the minor problems of plant evolution; concerning which principle some further observations may be offered.

The described involution of frond-plan belongs to one among several categories of homoeosis all subsumed under the larger type, but of this type it is a rather complicated example. A simpler illustration will make the nature of the general principle clearer, and at the same time exhibit its distinctness from another aspect of morphogenesis with which it is frequently confused—that of reversion.

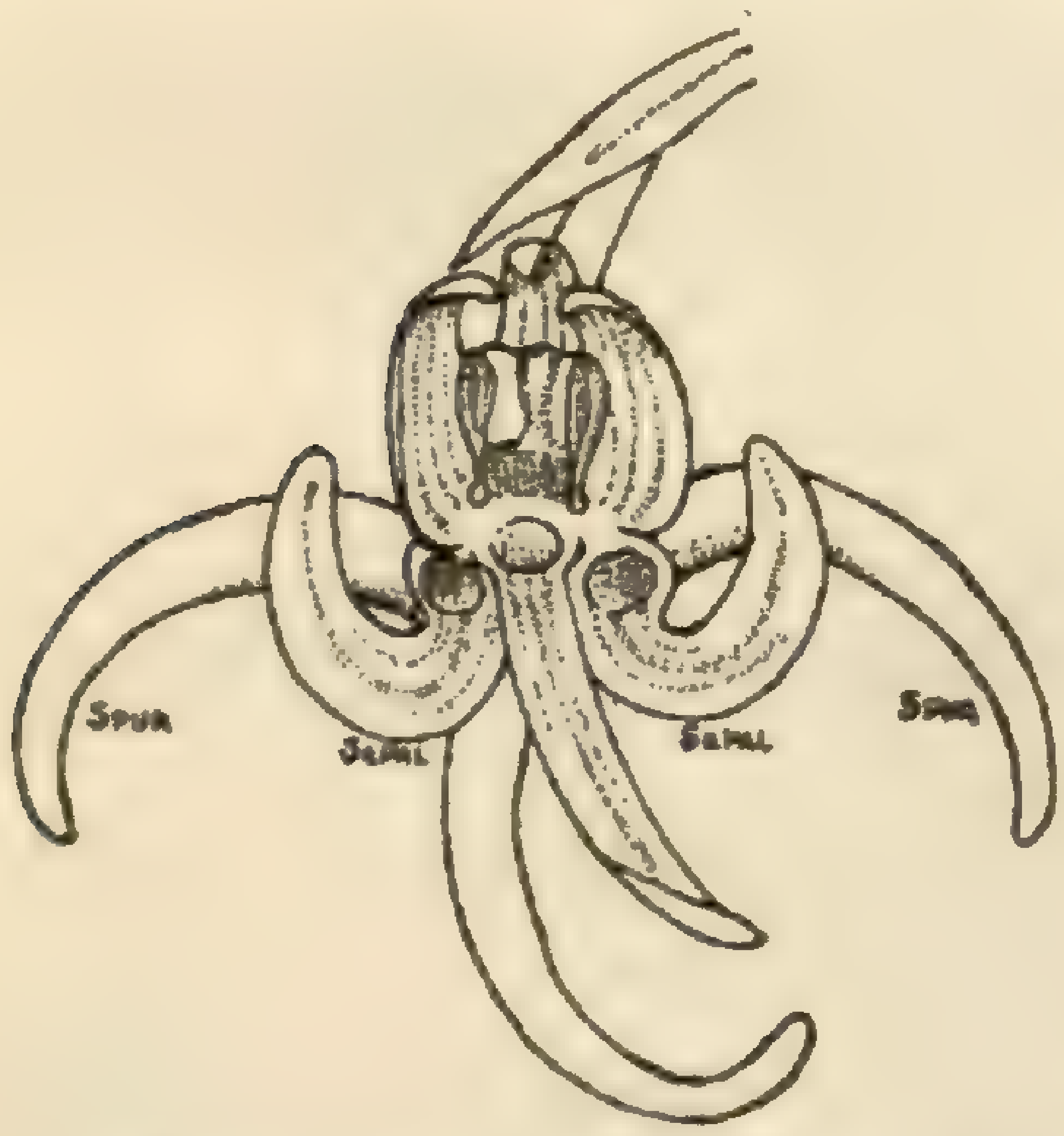

Fig. 5.—Abnormal flower of *Platanthera viridis*, with three spurs. After Hemsley.

In 1906 there was discovered in the county of Dorset, in England, a solitary plant of *Platanthera viridis*, the flower of which was remarkable for the possession of three spurs (*fig. 5*), one under the lip in the normal position, and one on each of the lateral sepals.[5] The extraordinary spurs entirely resembled the normal one. The general conformation of the flower was very nearly that of the species, though slight modifications were observable throughout.

The conditions of the occurrence make it highly probable that we have here the offspring of normal parents, rather than one member of a long series of gradually deviating forms; for in a botanically often- and well-explored country a race of deviants undergoing a gradual evolution from the typical condition of the species could hardly have escaped observation. It is necessary to suppose that the change of floral structure, in the line of descent embodied in this individual, supervened suddenly. The supernumerary spurs came into existence fully formed. They are not, however, new structures, except when regarded as sepallary appendages, and their origin morphogenetically and historically considered is easily discovered. The spur elaborated and perfected by the usual evolutionary processes—whatever the "usual" processes may be—as an appendage of the lip, has in a moment been transferred in full character to parts which heretofore have not been concerned—namely, to the sepals.

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[5] Hemsley, W. B., Journ. Linn. Soc. 38:3. 1907.

The principle is not new in biology. More than a century ago it began to be observed that when a part of such an animal as a worm is cut off, a new part different from that removed, but like some other part, may grow from the cut surface.[6] BONNET believed that there are special germs for the development of the various organs; as head-germs and tail-germs. From his experiments he made certain inductions concerning the distribution of these germs. LOEB[7] has investigated the conditions under which substitutions for lost parts may be induced, this process being regarded by him as essentially different from regeneration and deserving the distinct name heteromorphosis. LOEB also discovered that in some cases heteromorphosis can be produced without any organ being cut off, or any wound being inflicted upon the animal. Other investigators have dealt with the matter on experimental lines, especially with reference to the physiology of the process. WEISMANN has independently argued the translocation of characters from segment to segment in normal evolution of some insect larvae. He uses the word heterotopia in this connection.[8] BATESON, who appears to have discovered the principle in an original way in his study of variation, gave it the name homoeosis.[9] He describes cases in several phyla; for example, in Arthropoda the development of the extremity of a sawfly's antenna in the form of a foot; and in Vertebrata, the not uncommon anomalous presence upon the under side of turbots, etc., of the pigment and the tubercles proper to the upper side.

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[6] BONNET, CH., Oeuvres d'histoire naturelle et de philosophie 1:191, 215; 3: 247. 1779.

[7] LOEB, J., Studies in general physiology 115, 191, 627. 1905.

[8] The evolution theory (transl. by THOMPSON) 1:365, 367.

[9] Materials for the study of variation 85. 1894.

An interesting case in animals, which has lately come to my notice, is furnished by a crab, the claw being modified as shown in *fig. 6.* The superfluous claw, developed upon the normal dactyl, repeats in detail the style of the larger claw, as regards the general form and even the teeth.[10] The formation is believed not to be congenital, but to result from a wound to the normal claw near the time of moulting.

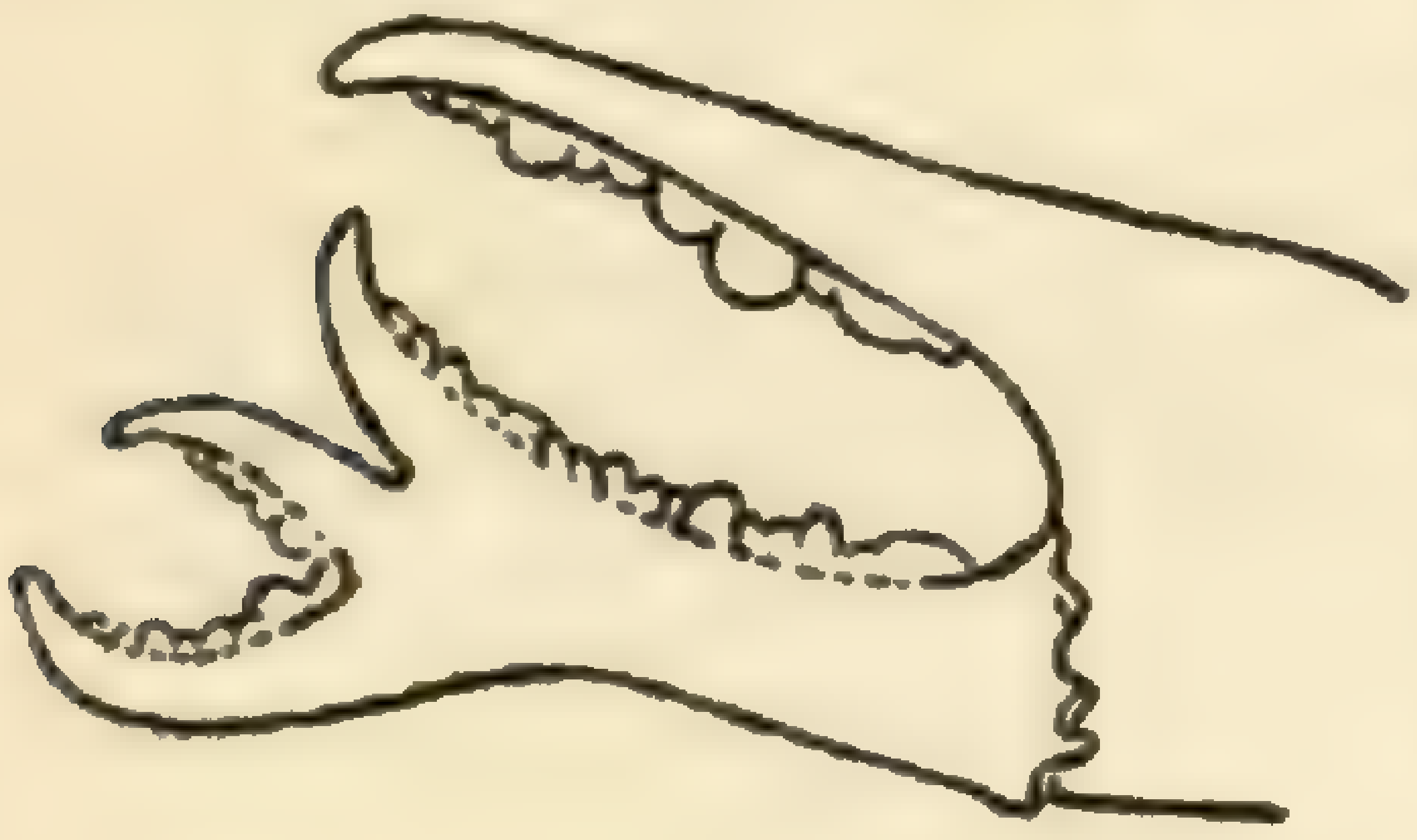

FIG. 6.—Crab claw, showing homoeosis.

The presence of the principle in animal development greatly enhances the interest which the botanical student of morphogenesis must entertain with respect to homoeosis.

In plants the transposition of organs has frequently been described in teratological works; but the phenomena of this class have been confused with those of a different nature, and the larger relations of homoeotic formations have not been recognized by teratologists. MASTERS devotes a short chapter to the subject, under the caption heterotaxy[11]—an expression which, as used by him, seems only in part to cover the ideas I am here endeavoring to formulate. MASTERS' chapter is a miscellany of teratological facts which will not go conveniently into any other chapter of his compendium. His term metamorphy[12] is too general for the present purpose, being employed

[10] Photograph in St. Nicholas Magazine **25**:177. 1907. The specimen is in my possession. A number of similar anomalies have been described by W. FAXON, Bull. Mus. Comp. Zoöl. Harv. Coll. **8**:257. 1881; by F. H. HERRICK in "The American lobster," Bull. U. S. Fish Com. 1895, p. 145, *pl. 47;* and by other writers of whose work a summmary appears in BATESON'S *Materials.* These authors do not specifically recognize the homoeotic nature of the anomaly.

[11] Vegetable teratology 156. 1869.

[12] It will be remembered that GOETHE employed the word metamorphosis in a different sense. SACHS, again, has a definition: "Metamorphosis is the varied development of members of the same morphological significance resulting from their adaptation to definite functions."—SACHS, Text-book of botany, tr. by BENNETT & DYER (1875), 131.

"to distinguish cases where the ordinary course of development has been perverted or changed" (p. 241). This author's *Vegetable teratology*, while it is a rich storehouse of facts for the study of homoeosis, is—as might be expected from the period of its publication—entirely wanting in illuminating discussion and appreciation of relations to the problem of organic evolution such as are to be found in Bateson. The latter author recognizes the presence of homoeosis in plants.[13] Sachs distinguished clearly between atavistic formations and those which are merely translocational. His explanation of the aberrations now being considered would indeed give a degree of literality to the expression *morphic translocation*, since he attributes them to changes in sap movement, with disordered nourishment and abnormal distribution of the formative stuffs.[14] Penzig's perception of the real nature of the anomalies now under discussion is clear.[15]

Modes of homoeosis in plants

In the vegetable kingdom homoeosis has many interesting phases, some of which I may indicate. The facts being superabundant, it is well to begin to categorize them, not for mere convenience, but in order that new and possibly suggestive points of view may be won.

1. *The translocation of characters may be acropetal.*

Everyone recalls numerous instances where details of the foliage leaves—toothing, texture, hairing, etc.—have appeared in the floral leaves. A case of acropetal translocation is that of the corolla fringe, peculiar to *Gentiana crinita*, from its normal site to the summit of the carpels.[16] A remarkable transposition has more than once been noted, of the secretory hairs (tentacles) of Drosera foliage to the sepals, petals, and even interior of the carpels.[17]

2. *The transference may be basipetal.*

Petaloid and sepaloid characters—color, texture, outline—not infrequently appear in the involucre, and sometimes the effects reach even the foliage. The most remarkable case that has come to my

[13] Bateson, *op. cit.* 111, 570.

[14] Stoff und Form der Pflanzenorgane, §3. Arbeiten Bot. Inst. Würzburg 2:452–488. 1882; also Gesam. Abhandl. Planzenphysiologie Bd. 2:1159–1231. 1893.

[15] Pflanzen-Teratologie 2:335, 489, etc. 1890–1894.

[16] Leavitt, Rhodora 7:14. 1905.

[17] Rhodora, *l. c.*; Planchon, Ann. Sci. Nat. Bot. III. 9:84, 86. *pls. 5, 6.* 1848.

notice occurs in a hybrid of the saffron (*Crocus sativus*). Stigmatic characters in this plant have wandered so far that not only the anthers and floral bracts, but also the foliage leaves are sometimes surmounted by portions of clearly characterized stigma, furnished with papillae; and even the sheaths below the leaves are tinged with saffron color.[18]

3. *Translocation may be lateral.*

Peloria, whether regular or irregular, illustrates this form of homoeosis. In the well-known *Uropedium Lindenii* (*Selenipedium caudatum*, Orchidaceae) the form of the remarkably long pendent petals invades the labellum, entirely subduing the saccate character of that member and converting the strongly zygomorphic into an actinomorphic corolla.[19] Contrariwise, the irregular member may impose its form upon the remainder of the corolla, as in the well-known peloric *Linaria vulgaris.*

4. *The invasion of migrating characters may be partial in any degree.*

The curious modifications of the pistil and its contents in abnormal *Drosera intermedia* illustrate this truth in several different ways.[20] As vegetative influences begin to evince their presence in the flower, the first modification of the gynoecium is an elongation of the ovary, especially its lower part. The carpels, while still concrescent, ovuliferous, and terminated above by the usual stigmatic apparatus, in a slight degree respond to the influx of foreign morphogenetic forces by the lengthening of their basal portions, corresponding to the petioles of foliage leaves: the carpels sensibly approach a petiolate condition. In flowers yet more affected the carpels separate in various degrees, finally falling apart altogether; their bases become elongated to form true petioles; the blades become more and more complanate and spathulate; the ovules after suffering a series of changes are finally replaced by tentacles; and the styles and stigmas, still retained even when the carpel-foliage-leaves spread horizontally from the center of the flower in rosette fashion, lose much of their rightful character. Thus is the gynoecium transformed step by step into a whorl of leaves. The metamorphosis of each part of the carpel is marked by the same flexibility and miscibility of characters which pertains to the whole gynoecium. In ovaries affected by the anomaly, but not yet resolved into separate carpellary leaves, ovules become stalked, the integuments may compose a small cup from the edge of which a few tentacles arise, or may be converted into minute modified discoid or concave leaf-blades bearing numerous minute tentacles. Between these blades, representing many characters of the radical leaves of the plant, and apparently perfect ovules, many stages of gradation have been observed. Similarly the stigmas and styles, in the most aberrant carpels, combine with their own characters the structure of marginal tentacles.

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[18] CHAPELLIER, P., Journ. Royal Hort. Soc. **24**:277. 1900.

[19] LINDEN, L., Pescat. *pl. 3;* REICHB. F., Xen. Orch. **1**:*pl. 15.*

[20] PLANCHON, *l. c.* 86.

The accompanying *fig. 7* represents advancing petaloid modification of the calyx of *Ranunculus bulbosus*. The normal sepal *A* is green and hairy on the back, while the petal is glabrous and yellow. Sepals *B*, *C*, and *D* are progressively invaded by yellowness and glabrousness (and doubtless by other corolla characters), until in *D* all that remains of sepal nature is hairiness and slight greenness in the median line of the back.

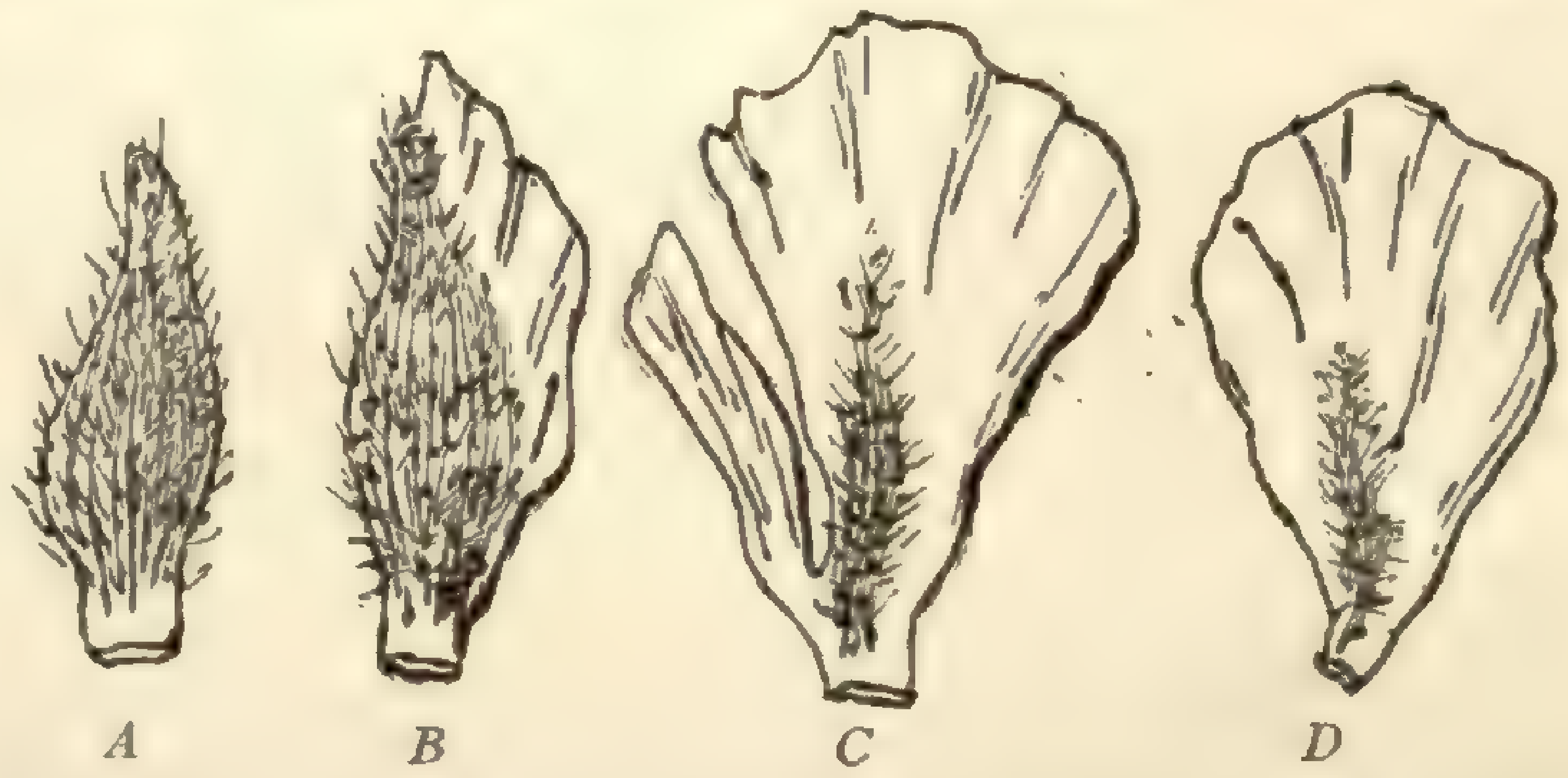

FIG. 7.—Progressive homoeosis in sepals in *Ranunculus bulbosus*. After O. AMES.

The intermediate formations described here, which are of very common occurrence in plants, are the "anamorphoses" of CELAKOVSKY.

5. *Migrating characters may transgress boundaries of homology.* The term "homologous," applied to organs supposed to have had a common evolutionary origin, is very often vague and not rarely is practically meaningless for the reason that, while degrees of homology are infinite, the specific degree of homology in many cases cannot be known even approximately. In spite of this vagueness in the word, however, most botanists will probably agree that the ovule is in no just sense the homologue of a shoot, nor yet of a pistil, nor of a stamen, nor of a foliage leaf, nor of the droseraceous tentacle. Yet

the fundaments of ovules have been observed to develop into all of these structures. LEITGEB reported[21] a *Marchantia polymorpha* in which cupules of various degrees of development (presumably with gemmae) took exactly the places of archegonia. Yet cupules and archegonia are not homologous.

6. *When against homology, the invasion may be partial in any degree.*

Without entering into details, the literature of ovular abnormality may be cited in support of this opinion.[22] Even when the imitating and imitated structures are known not to be related historically, the presence in any organ of form-giving factors derived from a different organ may merely be indicated by some faint resemblance, or may be pronounced in any degree up to the total replacement of the local member by the foreign.

A corollary of the above propositions (5 and 6) may be stated: Homology of two organs cannot be inferred on the ground alone of the replacement of the one by the other, or of the translocation of features proper to the one into the other of the organs. The existence of even a so-called "complete" series of gradations between two members does not necessarily imply the homology of the members. I think that the anamorphoses of CELAKOVSKY have not the extraordinary phylogenetic significance, as compared with other kinds of abnormality, which this author has attributed to them.

7. *In homoeosis characters may pass from one to the other of the alternating generations.*

YAMANOUCHI has recently published[23] an account of the very interesting conditions attending apogamy in *Nephrodium molle*. The apogamous prothallia bear no functional archegonia, but they proceed to initiate the sporophyte directly. A superficial cell on or near the cushion divides perpendicularly to the surface, and underlying cells divide in various directions. From the complex so originated, the sporophyte develops. The cytological history being followed throughout the critical stages, no nuclear fusions were found; and as a matter of fact the chromosomes of the sporophyte continue to be of the reduced (or x) number. Here we have a sporophytic form imposed homoeotically upon a gametophytic cell basis.

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[21] Bot. Zeit. 33:747. 1875.

[22] WIGAND, A., Grundlegung des Pflanzen-Teratologie 39. Marburg. 1850; MASTERS, *op. cit.* 186, 262–271; WYDLER, Denkschr. Regensb. Bot. Gesells. 4:77. 1859; PLANCHON, article cited; CELAKOVSKY, Bot. Zeit. 33:129–177. 1875. etc.

[23] BOT. GAZETTE 44:142. 1907; 45:289. 1908.

The contrary or aposporic case in ferns has been studied in detail by several workers. In *Athyrium Filix-foemina*, BOWER[24] found the sporangia arrested at various stages, the development being carried on by prothalloid growths which organized typical wedge-shaped cells at one or more points on their margins, while rhizoids were formed at the same time by the outgrowth of individual cells. DRUERY[25] had already observed sex-organs and even young plants arising from these prothallia. WOLLASTON[26] found in *Polystichum angulare* that the tips of pinnules were converted directly into prothallia, bearing archegonia and antheridia. In these cases a gametophytic form is imposed homoeotically upon a sporophytic cell basis (with little doubt; though the cytology, I believe, has yet to be worked out).

Entirely parallel is the production of protonemata from the setae of mosses, as observed by PRINGSHEIM[27] in Hypnum and Bryum, and by STAHL[28] in Ceratodon. LANG[29] has demonstrated the power of Anthoceros capsules to produce thalli aposporically.

The adventive structures are, of course, gametophytic, yet they arise by the prolification of sporophytic tissues.

8. *When the boundary between alternative generations is so transgressed, the invasion of extraneous characters may be partial, and both generations may be represented side by side in the same body.*

GOEBEL[30] has recently induced the formation of prothalloid growths from cut fronds of very young plants in several species of ferns. Some of the aposporous prothallia bore stomata, as well as sex organs (p. 132). LANG[31] found sporangia in various stages of perfection, produced in groups having a superficial resemblance to sori, upon prothallia of *Scolopendrium vulgare ramulosissimum* which had been growing for a long time without fertilization. LOWE'S cultures of *Scolopendrium vulgare* exhibited the combination of alternative generations in an interesting manner.[32] "We have here consequently a position as nearly as possible intermediate between sporophore and oophore, the sporophoric character distinctly existing in the shape of a circle of stalked fronds generated spirally from a regular axis of growth, while the oophoric character as distinctly appears in the fact that these fronds are practically stalked prothalli bearing the sexual apparatus proper to them."

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[24] Journ. Linn. Soc. 21:360. 1886.

[25] *Ibid.* 21:354. 1886.

[26] As reported by BOWER, *l. c.* 362.

[27] Monatsb. Akad. Wiss. Berlin, July 10, 1876.

[28] Bot. Zeit. 34:689. 1876.

[29] Annals of Botany 15:503. 1901.

[30] Sitzb. Bayer. Akad. Wiss. 37:119–138. 1907.

[31] Phil. Trans. Roy. Soc. B. 190:194. 1898.

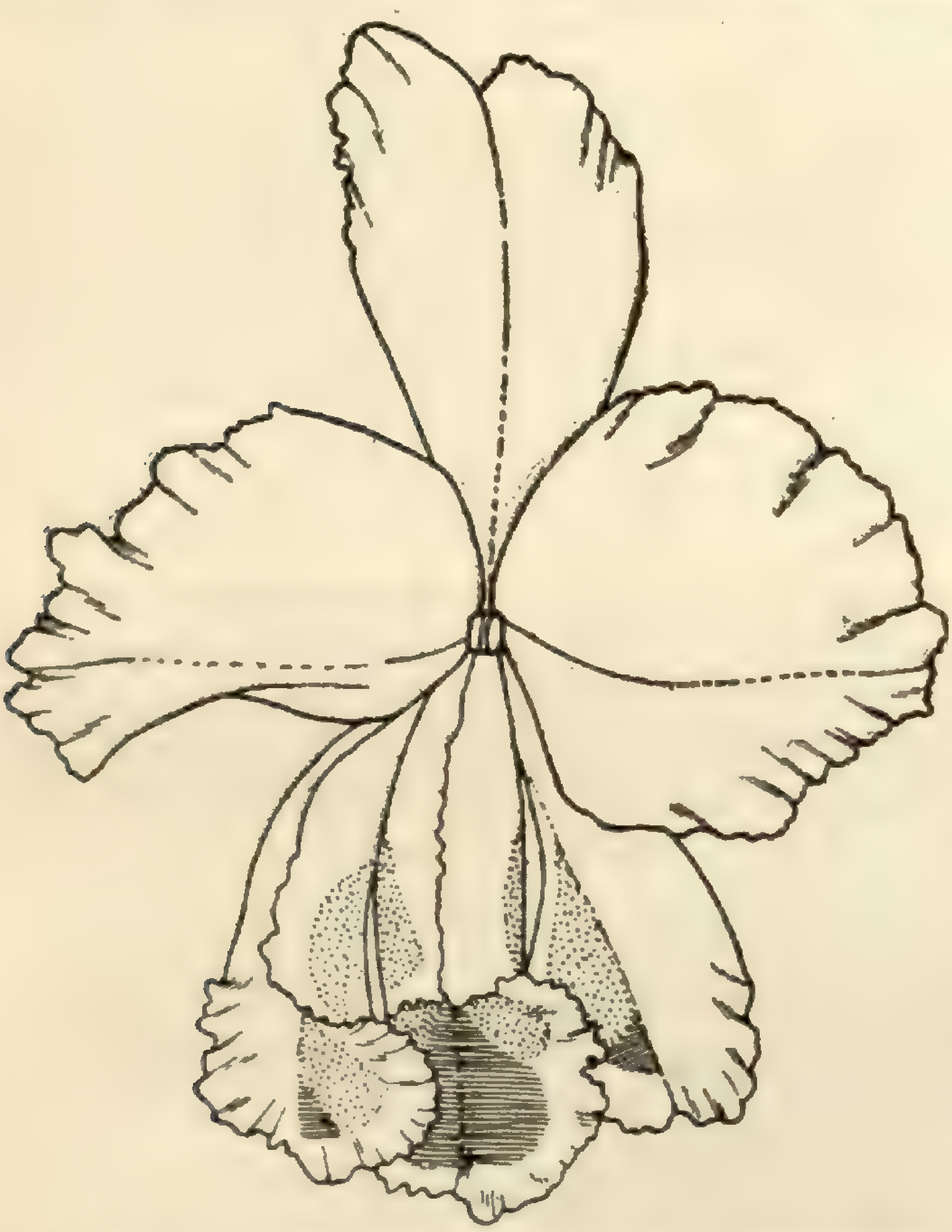

FIG. 8.—Abnormal flower of *Cattleya labiata*. After a colored drawing by O. AMES.

9. *The exact character of a homoeotic metamorphosis is often determined by the nature of the nearest normal organs.*

In many cases proximity appears to be a predominant factor. The following instance conveys more definitely the meaning of this general statement. A plant of *Cattleya labiata*, formerly grown in the greenhouse annexed to this laboratory, produced flowers uniformly exhibiting petaloid homoeosis of the calyx (*fig. 8*). The three sepals—which in normal flowers are rather narrowly lanceolate—were broadened, and their margins were crisped in imitation of the

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[32] Journ. Linn. Soc. 32:536. 1896. The quotation above is from DRUERY'S report in Mr. LOWE'S communication.

ovate crispate petals. The two lateral sepals, however, differed from the dorsal in that the inner half of each became colored like the labellum. The latter organ forms in this species, by the inflection of its margins, a loose tube, embracing the column, open distally and expanding to form the landing-stage for the pollinating insect. The floor of the tube has a broad yellow stripe, widening toward the mouth, and at the extremity replaced by a large purple or crimson-magenta patch. These colors are bounded by the pale magenta body-color of the flower. In the abnormal specimens the halves of the lateral sepals next the labellum reproduced the color-pattern of half the labellum. The halves away from the labellum were like the rest of the flower in hue. This peculiar distribution of the colors becomes interesting when an examination of the base of the perianth shows that in *Cattleya labiata* the foot of each lateral sepal is close to the foot of the labellum and overlaps it by just half—the half corresponding to the homoeotized half-limb in the abnormal flowers; while the other perianth segments stand somewhat apart from the lip. In these particolored sepals the discrimination between homoeotic and non-homoeotic areas seems to be directly related with contiguity to the "source" of the derived features.

PENZIG[33] has dwelt upon this phase of the phenomenon which we are now calling homoeosis, in his general considerations of the significance of monstrosities and in his arguments for the theory of DELPINO regarding the nature of the fertile scale in Abietineae. He was impressed, as everyone must be, with the agreement between the facts of this category and the formative-stuff theory of SACHS.

10. *A compound member may be changed in such a way that some or all of the parts exhibit the plan originally characteristic of the whole member* (*entropic homoeosis*).

The general plan of organization is transferred from the member as a whole to the constituent parts. Compound members may thus, by an entropism of form, suddenly become decompound. This form of homoeosis has already been illustrated in the description of the Pierson fern above. Further examples in leaves of ferns and flowering plants may be noticed here, since this variation has an interesting relation to the question of the evolutionary origin of compounding;

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[33] Pflanzen-Teratologie, *l. c.* (and elsewhere).

and besides is interesting from the purely morphogenetic point of view. The same species of variation is also to be observed occasionally in inflorescences.

A glance into two or three private and as many institutional herbaria makes it evident that entropic homoeosis is prevalent in ferns. I have found it in the ten species following, repeatedly in several of them: *Aspidium Thelypteris*, *A. spinulosum*, *Polystichum acrostichoides*, *P. angulare*, *P. Braunii*, *P. munitum*, *Asplenium thelypteroides*, *Dicksonia punctilobula*, *Polypodium vulgare*, *Osmunda cinnamomea*.

Among these species I have found the phenomenon most frequently in *Polystichum* (*Aspidium*) *acrostichoides*, in which species its operation takes some interesting turns. The fronds of *P. acrostichoides* are somewhat dimorphic, not only in the sense of being soriferous and non-soriferous, but also in the fertile and sterile fronds having slightly different general outlines. The sterile fronds have their apical pinnae non-auriculate, obtuse and oblong or elliptical to obovate. In the fertile fronds, the pinnae, again, are dimorphic, the apical ones being shorter, narrower, and abundantly soriferous. Homoeotized pinnae which I have found on various specimens represent the entire range of this dimorphism. A specimen in the herbarium of A. A. EATON, ex-herb. E. J. WINSLOW, collected in Lowman, Chemung Co., N. Y., has the two basal pinnae transformed into miniature fronds. Their length and breadth are increased, and the segmentation is quite perfect. One of them very nearly represents a fertile frond, its terminal portion being constricted and soriferous, and many of the pinnules being auriculate or toothed (*fig. 9*). Some of the pinnules,

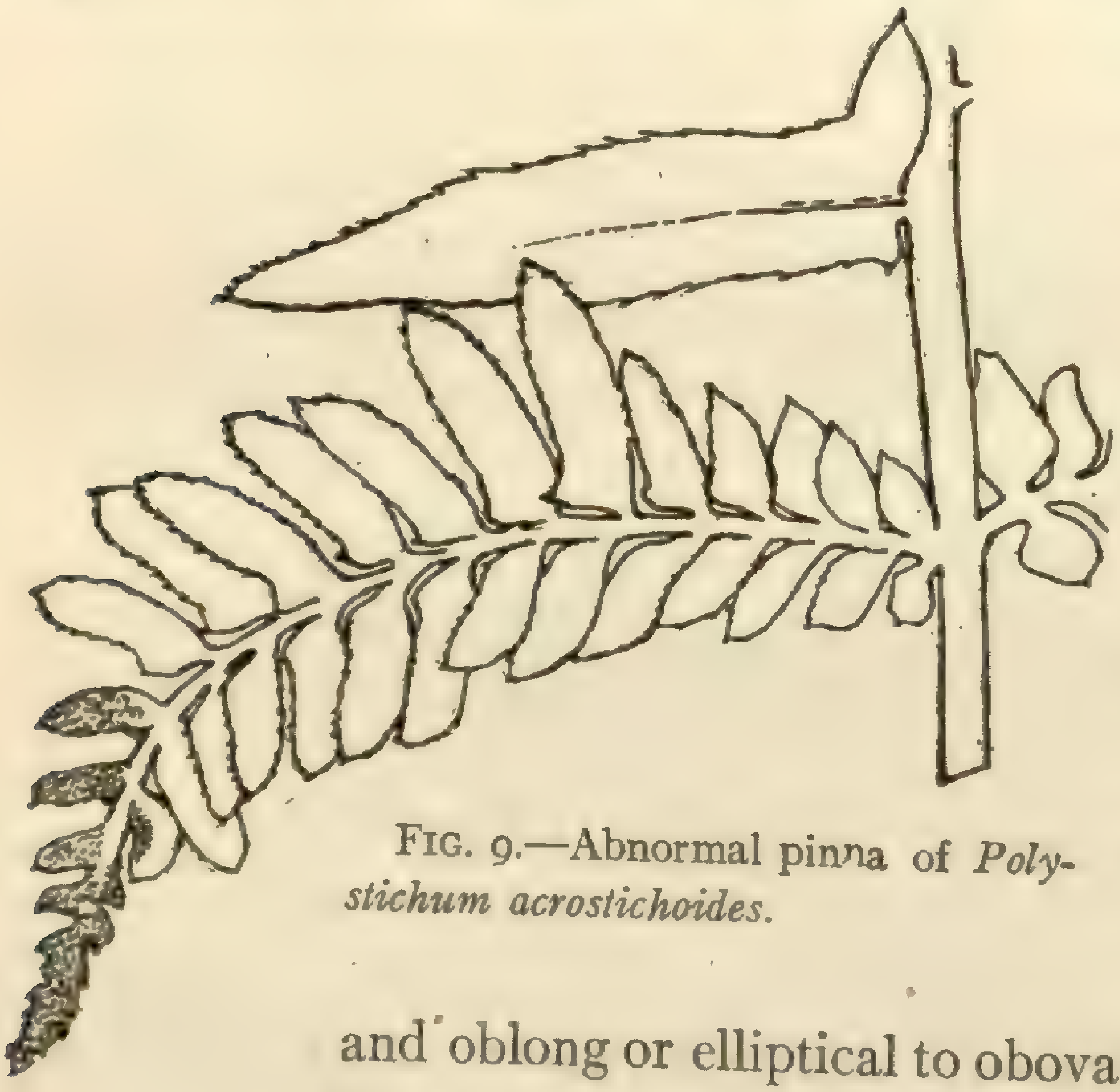

FIG. 9.—Abnormal pinna of *Polystichum acrostichoides*.

however, are of the type found toward the extremity of the infertile frond, as above described. The proximal fourth of this pinna is occupied by pinnules much shorter than the rest, so that the total width of the pinna here is about normal. This region is the part of the pinna corresponding to the stipe of the frond, and would be bare of pinnules were the frond-plan fully realized; as a matter of fact two form-forces are expressed, the pinnar, which gives a blade of proper width on either side of the mid-vein, and the frondescent, which divides the blade. In the opposite basal pinna of this specimen, segmentation is complete, but the homoeosis refers to the terminal pattern of the sterile frond.

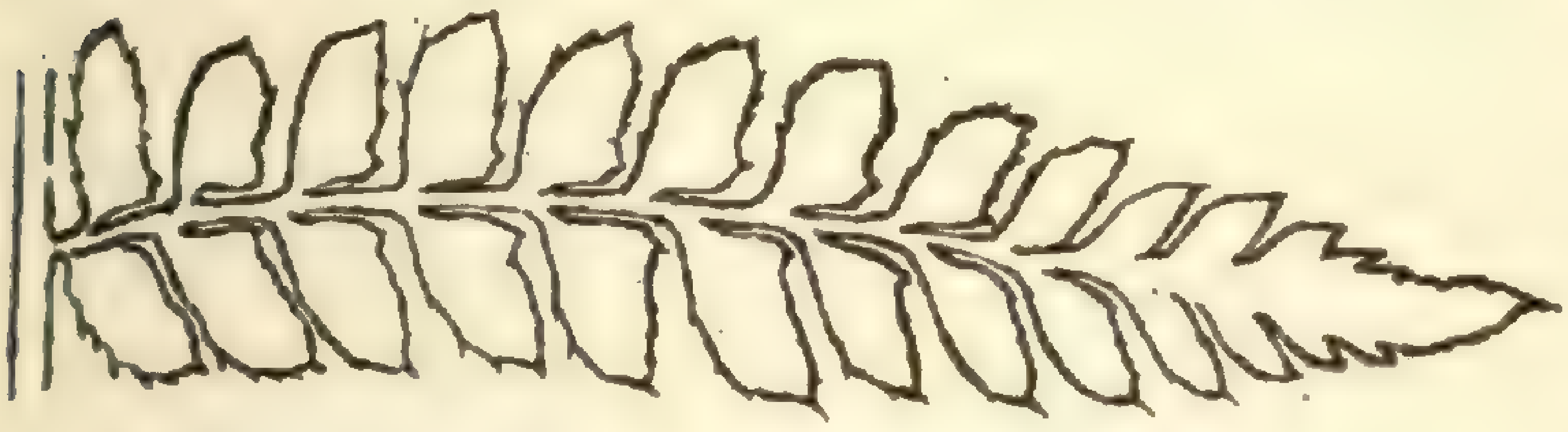

Fig. 10.—Normal pinna of *Polystichum Braunii.*

A specimen of this species in the Gray Herbarium marked "Herb. A. Gray. Near Philadelphia, Bourguin," exhibits an interesting interplay of form-factors, wherein that which at first sight appears to be extreme irregularity gradually resolves itself into definite adherence to pre-existing types. Frond-plan in the pinnae is expressed by segmentation and by the character of the segments, by their increased length, and by increased width of the distal two-thirds, and in some of the lower pinnae by the absence of pinnules from the lower side of the pinnar rhachis, throughout the basal one-third or thereabouts of its length—in an "effort" to realize the petiolate condition of a frond. The segments, more or less complete, are those of the apical region of the infertile frond of the species, and the frond-form, in so far as it is realized in the pinnae, is of the infertile type. In these pinnae, the old fashion (pinnar character)

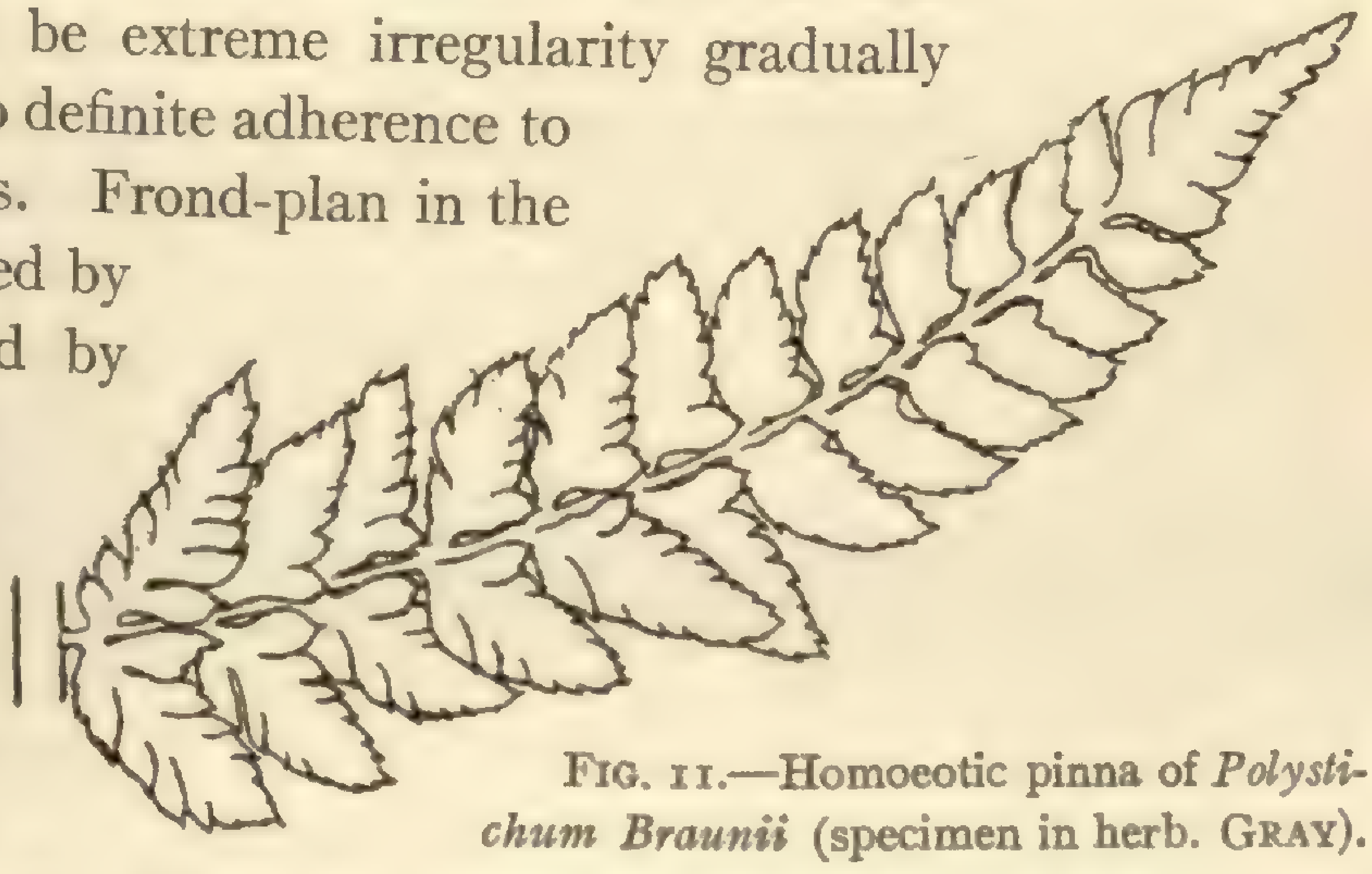

Fig. 11.—Homoeotic pinna of *Polystichum Braunii* (specimen in herb. Gray).

is able to express itself simultaneously in the morphogenesis, by more or less successfully reducing the segmentation, by maintaining normal width in the basal region of the pinna, and by accentuating the basal segment on the upper side of the pinna, in correspondence with the large tooth or auricle which stands there in normal pinnae. The homoeotic character of the variation is unmistakable, though partial.

In a specimen from the Torrey herbarium, at the New York Botanical Garden, the frondescent pinnae of the lower section of the aberrant frond imitate an occasional trick of the species, by which soriferousness may run down the margin of the sterile region, on the tips of the pinnae. In the Torrey specimen, the lower frondlets (pinnae) are soriferous and constricted in their apical region, and the soriferousness runs down their margins on the tips of the pinnules.

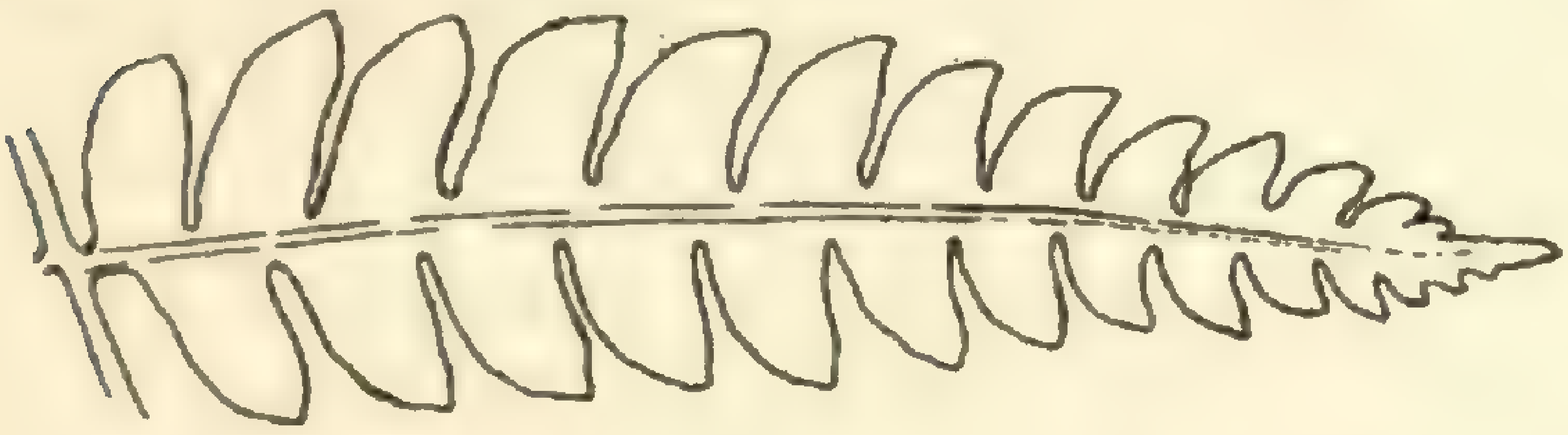

FIG. 12.—Normal pinnule of *Osmunda cinnamomea.*

Dicksonia punctilobula in the herbarium of Mr. F. G. FLOYD shows entropic homoeosis of an interesting type, inasmuch as the primary segments become frondescent in imitation, not of the adult but of the infantile, or nepionic, leaves.

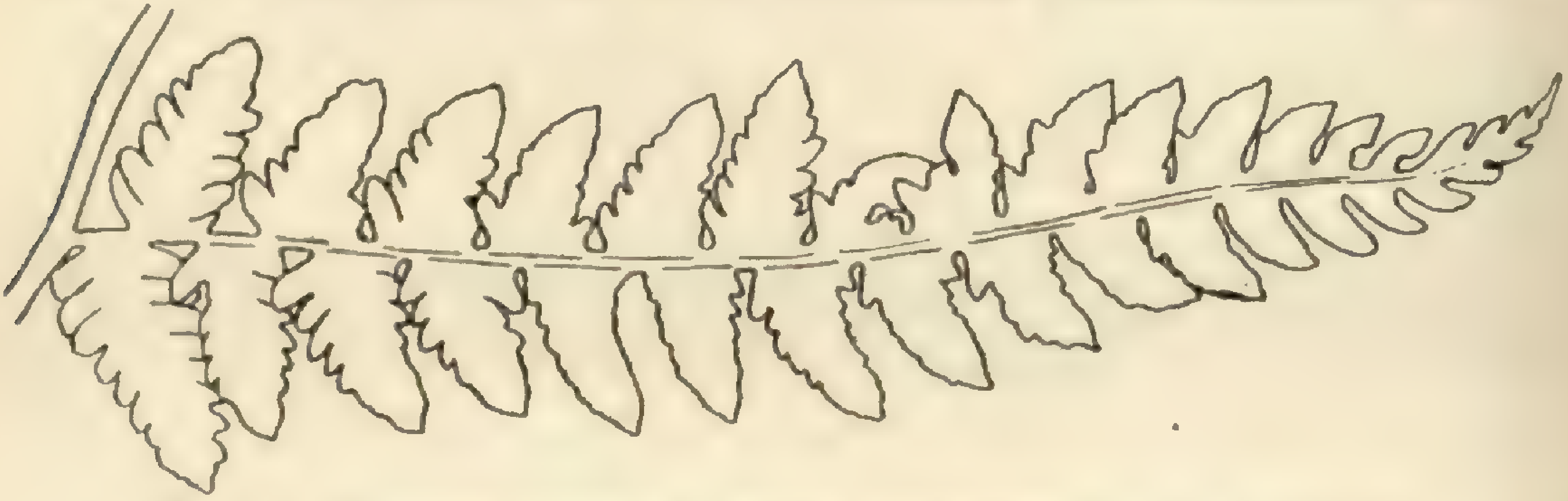

FIG. 13.—Homoeotic pinna in *Osmunda cinnamomea* (in herb. FLOYD).

Asplenium thelypteroides collected by DAVENPORT and FLOYD at Coon Hollow Brook, Milton, Mass. (hb. FLOYD), has the second and sixth pinnae frondescent (others in a less degree), the modification proceeding upon the basis of the lobing already normally present in the pinnae, and resulting in the formation of segments of a secondary rank imitating the normal primary segments; and further, in a change in spacing of the divisions, which brings the modified pinnae into conformity with the main frond-plan as regards the distance of the segments. Increased spacing, correlated with perfected divisions, in very obvious homoeosis, is also seen in *Osmunda cinnamomea* (*fig. 13*) collected by F. G. FLOYD at Mt. Desert, Me., where, according to the collector, the form is evidently hereditary, numerous modified plants covering a considerable area.[34]

Coming to flowering plants, the principle is seen in curious variations of the leaves of an Aster which Mr. C. STUART GAGER has kindly shown me. They were briefly noticed by him in *Torreya* for January, 1908. Basal laciniae have become increasingly distinct, some of them even petiolate (petiolulate); and when so, the new, or secondary, blades imitate the main blade, even down to a peculiarity of asymmetrical development.

I regard a leaf condition found by me in *Gleditsia triacanthos* as homoeotic. At any rate the variation noted is very abrupt. The character leaf of the species is simply paripinnate, the leaflets short-stalked, the blade slightly unequal at base, elliptical, obscurely serrulate or crenate, apiculate. In the leaves of vigorous running shoots (not spur shoots) I find some of the leaflets replaced by segments imitating the normal leaf in all the features specified above; the segments are, in effect, character leaves of a second order. The modified, or compound, leaflets, which are nearly twice as long as the unmodified ones, occur irregularly among the others (*fig. 14*). The condition here, essentially the same as that described for the Pierson fern, has been noticed also by GAGER (*l. c.*), one of his specimens—as also one of mine—carrying the homoeosis to the second degree, a few *pinnules* becoming perfectly compounded (as in the Whitman fern). There is no evidence, so far as I know, that the modified condition looks back to an older, normal state of division. What happens is that segments of the leaf are transformed into the likeness of something now existing—the normal, or character, leaf of

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[34] Examples of entropic homoeosis may be found in MOORE and LINDLEY, The ferns of Great Britain, etc., Nature printed. London. 1857; and in MOORE, Nature printed British ferns. London. 1859 (?).

Mo. Bot. Garden
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the species. The likeness is perfect. Whether the variation here is admitted to be at the present time in each instance a fresh display of homoeosis, or is suspected of being reversionary, the abruptness of the change and the manner of its occurrence seem to me plain indications of the origin of the decompounding. It seems to me far more likely that this is entropic homoeosis, past or present, than that the complex form of the compound segments was worked into perfect likeness to the original blade slowly by natural selection.

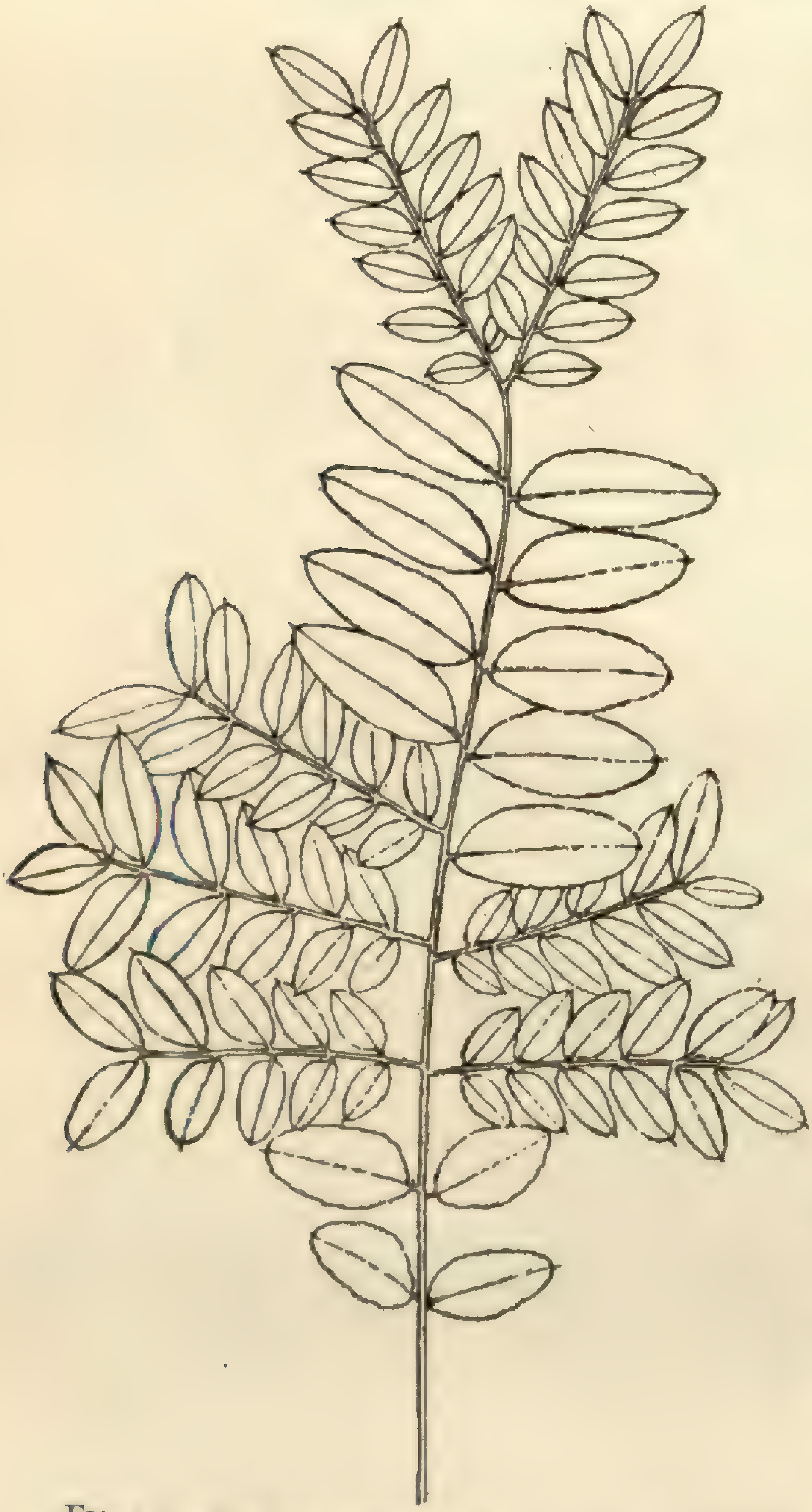

FIG. 14.—Leaf of *Gleditsia triacanthos* with seven homoeotic pinnae.

BONNET recorded a variation of the jasmine (*Jasminum officinale*) which is seen to be homoeotic in a similar way. *Fig. 15* shows the normal and variant forms side by side, as delineated by BONNET (Oeuvres **2**:363. *pl. 24*).

Inflorescences of certain marked types sometimes undergo entropic homoeosis; for example, umbels and pseudumbels. Of the former I have seen two cases, the first in *Aralia nudicaulis* (specimen in hb. N. Y. Bot. Garden, coll. by AUSTIN C. APGAR, near Lambertville, N. J., 1887). This species normally bears simple umbels at the ends of the three main branches of the scape. In APGAR'S specimen some of the florets in each umbel are replaced by long-pedicelled umbellules. That is, the form resident in the flower cluster as a whole has instantly passed into several of the parts (florets). A similar variation I have seen in *Hydrocotyle umbellata* (specimen in hb. N. Y. Bot. Garden, Jamaica, FERRY, no. 6168); and in *Daucus Carota* it was noted by CRAMER,[35] radial florets being replaced by umbels.

Two false umbels of Pelargonium in my possession are abnormal in a similar way. In each case one of the florets, eccentrically situated, has been transformed homoeotically, with the result that it rises as a pseudumbel of a secondary order from amid the flowers of the first. The subordinate flower cluster is like the chief cluster as regards centrifugal development, involucre, etc., though the flowers are fewer (8 instead of 18) and shorter-pedicelled. The secondary peduncle is articulated to the expanded summit of the primary, as are the pedicels of the flowers, and apparently would have been cast off, in event of failure to fertilize, by an absciss-layer, as with the flowers among which it stands.

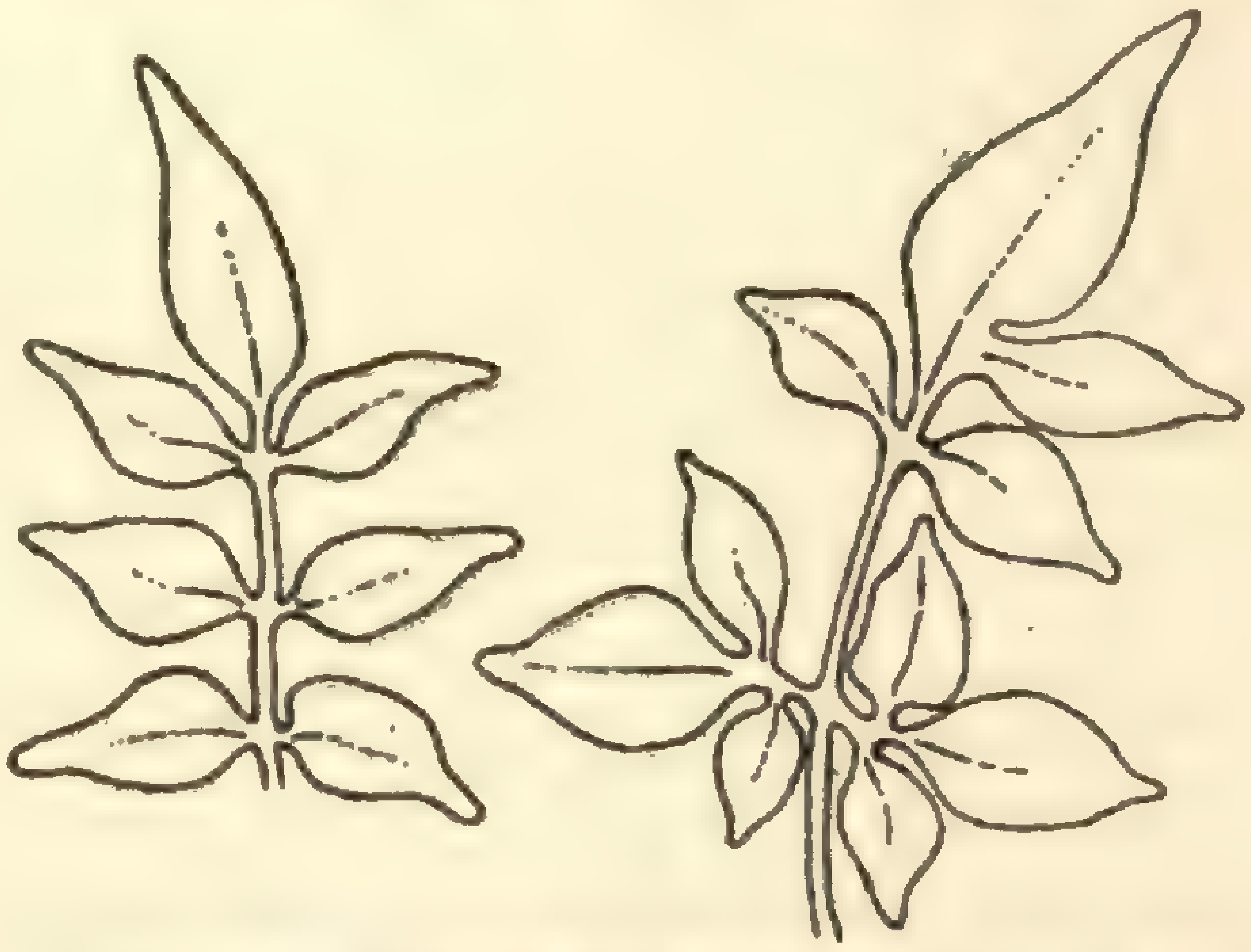

FIG. 15.—Normal leaf of jasmine (left) and a leaf with homoeotic segments (right). After BONNET.

Homoeosis and reversion

I have said that homoeosis is often confused with reversion; indeed among botanists the confusion may be said to have been habitual. The older writers having applied to homoeotic phenomena the word reversion in its ancient sense, some contemporary authors have with little reflection retained the antiquated language in expressing ideas which are altogether modern.[36]

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[35] CRAMER, C., Bildungsabweichungen bei einigen wichtigeren Pflanzenfam., etc. 63. Zurich. 1864.

[36] In Rhodora 7:18, 19. 1905, I have discussed briefly the origin and use of the reversion idea as applied to plants.

In order that the real relations of the forms concerned shall be more generally recognized, one needs but to direct attention to them; argument is scarcely needed. For example, the appearance of two supernumerary spurs in *Platanthera viridis* is palpably anything but atavistic. No one at all conversant with Orchidaceae will for a moment imagine that there ever was an ancestral race of three-spurred Habenarias to which the curious Dorset plant harks back. In the above-mentioned gentian with the fringed carpel, the relation of things in evolutionary time is perfectly clear. While the carpel is an ancient, the fringe is a very recent, structure; the former was not derived from a petal, and the fringe has never until now been a carpellary appendage. When the carpel puts on the fringe, therefore, it adopts a character not to be found in its own phylogenetic line. Simply the fringe is borrowed; there is no reversion. The non-atavistic nature of the stigmatic papillae on bracts and foliage of *Crocus sativus* is equally patent. The assumption of foliage characters by carpels of Drosera is no more reversionary. The carpel of Drosera, it is safe to say, had its origin in common with that of other angiosperms, and runs back through a series of forms, none of which is a foliage leaf, to the megasporophyll of the earliest angiospermous seed-plants. Likewise the foliage leaf of Drosera is a derived structure, with characters probably more recent than the family Droseraceae even. Its peculiarities of contour and its appendages arose long subsequently to the establishment of the angiospermous, and even the droseraceous, carpel. To reach a point whence these two lines of derivation diverged, i. e., a point where the reproductive and the vegetative organs were one and the same member of the plant body, we must probably go back to the spore-bearing foliage leaf of the fernlike ancestry, far antedating the first flowering plants. The common original of the Drosera carpel and the Drosera foliage leaf was probably a kind of fern frond. The aberrant carpels in question bear no resemblance to fern fronds. They do not reproduce a form from which they are descended. They have simply taken to themselves properties of coordinate derivative members, the foliage leaves. This is so obvious that the statement would seem superflous were it not still the custom of inconsiderate writers to speak of such metamorphoses as reversions in the phylogenetic sense. The transformation is not retrograde in any except an imaginary sense; since the normal unmodified carpel is to be regarded as already "retrograde," or conservative, as compared with the tentaculiferous leaf; and the ovule as vastly more ancient than the tentacle into which it suffers change.

In peloria the morphogenetic relations are not so instantly obvious. However, the phenomenon is usually, if not always, better viewed as a homoeotic, than as an atavistic, occurrence. In notices of peloric monstrosities one often meets with the statement that these formations have a historical value. Thus, with respect to a peloric Laelio-Cattleya, MASTERS[37] suggests that here is a reversion to the earlier and simpler conformation from which the peculiar orchid structure, as we know it, has evolved. While this is true abstractly, in a merely descriptive sense—since actinomorphy doubtless preceded zygomorphy in the monocotyledonous phylum—yet it is probably untrue if we are to take it in any real phylogenetic sense, with the understanding that actinomorphy has remained latent as a hereditary character through the enormously long period of the evolution of this family from an actinomorphic condition. Regular peloria is to be considered in conjunction with the opposite change, which frequently occurs in orchids. The antithesis of the two pelorias makes it evident that we have here something besides atavism; since if either form is atavistic the other cannot be. This outcome, coupled with the fact that we have a less objectionable construction, discredits the entire idea of reversion in peloric orchids. The argument extends to other families.

Without further expatiation, it will be evident—if the standpoint of the present paper is correct—that the word reversion is a much-abused term. True reversions, except those which occur periodically in the ontogenesis, are, I suspect, rather rare. Atavism is never to be assumed off-hand in teratological cases, but it is to be admitted only when established by aid of independent proof. It should be borne in mind that *antecedents of monstrous forms are much more often to be sought in contemporary normal parts than in ancestral conditions.*

The place of these facts in botanical theory

The facts to which I am referring from a special point of view have values in botanical theory in at least three different relations:

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[37] Gard. Chron. II. 31:235, 239. 1902.

first, a study of the modes or phases of homoeosis helps us to estimate at its true worth teratological evidence applied to the solution of phylogenetic problems; *secondly*, the facts seem to throw light on the method of evolution of some normal structures; *thirdly* and chiefly, the facts of homoeosis constitute, as has been already pointed out in the introductory passage, an important section of the data of morphogenetics. Let us examine these relations of the subject a little more in detail.

1. The study of homoeosis must somewhat increase the caution with which we use deviations from the normal as aids to morphological interpretation.

In the past the commonest use of abnormalities has been to make them the ground of phylogenetic inductions. The stereotyped remark of writers describing monstrous specimens has been that such aberrations "are very instructive"—an expression of faith either in the phylogenetically reversionary nature of abnormalities, or in the eternal inviolability of homology in morphogenetic sequences. Surmises from monstrosity alone were naturally more common in the days when the evolutionary story of plants was less complete than it is now, and when morphologists were driven to indirect and speculative methods. The history of this subject is voluminous; perhaps, though interesting as a study in speculation, it is more valuable for the errors which it embodies than for any content of truth; and it will not be entered into here. Some of the contentions for which teratological formations were used have been abandoned, and others have been settled by the discovery of direct evidence from comparative morphological studies of living and extinct plants. As we are enabled by extension of knowledge and maturing of opinion to understand better the relations of both normal and abnormal forms, it becomes evident that the imagined morphological significance of many abnormalities falls to *nil*. For example, we now know that the conversion of the nucellus of an ovule to a shoot, as in Aliaria and in Drosera, is wholly without phylogenetic meaning. From a study of even normal organization we are losing the belief of earlier botanists in the absolute integrity of morphological categories; and if the observations assembled in the present essay are accepted in the sense in which they are presented, it is indisputable that stages of development supposed to be concatennated in a fixed order are subject to the most violent dislocation—that a stage belonging to one morphological category may pass into another of a different category.

Abnormalities which are traceable to very ordinary features of contemporaneous organization and may be brought under the rule of homoeosis, will for the moment lose all historical force which they may ever have been thought to possess. Historical significance can be restored to them only by application of the laws (if we may so speak of the operations) of homoeosis. If homoeosis much more easily follows lines of homology, and only rarely transgresses them under very special conditions, then frequent homoeotic metamorphosis of a particular organ in a particular direction may be thought to be indicative of the derivation of the organ. But I think that the admission of homoeosis in any case is practically fatal. The method of inference then becomes too roundabout to be acceptable to modern taste. If in any case homoeotic formations agree with the results of comparative morphology, of anatomy, and of organogeny, still they add only a reflected light to the general illumination.

In writing these words I have in mind particularly the long debate over the morphological nature, or origin, of the ovuliferous scale in conifers; or so much of it as relates to malformations. Perhaps no single organ of vascular plants has afforded morphologists more matter for disputation than this scale, which has a vast literature of its own by the most eminent authorities—LINNAEUS, A. BRAUN, SCHLEIDEN, VON MOHL, EICHLER, SACHS, BAILLON, STRASBURGER, VAN TIEGHEM, DELPINO, PENZIG, MASTERS, NOLL, CELAKOVSKY, and others. The theories of these authors have been various, and based upon every conceivable consideration, not least upon abnormalities. Teratology has appealed very differently to different students—to some as supporting one doctrine, to others as favoring a different theory; to some as of great or even decisive weight, to others as having no significance at all. CELAKOVSKY, who has studied the matter most persistently, has relied upon abnormalities, and especially upon unbroken series of intermediate formations, such as those between the fertile scale as it separates into parts (at the appearance of a shoot) and the leaves (or bud scales) of the shoot. This author assumes that such gradations can exist only between homologous organs. He regards the entire composite structures found in the monstrous cones, made up of the fertile scales and the shoots which grow through them, as such intermediate formations (anamorphoses), and looks upon them as sufficiently proving the shoot-nature of the fertile scale.[38]

From the numerous clear and detailed drawings of the abnormal cones which have been published,[39] certain truths are apparent enough. First, no new organ or form of any organ, not proper to the species of today, except intermediate formations between present-day vegetative and reproductive parts, is to be found in the cones. No ancient structure, nor anything suggesting ancestral structures, nor any organ of paleobotanical aspect, makes its reappearance out of the past; there is no reversion. If the shoot in the axil of the bract, replacing the scale, were truly atavistic, we should expect that lost characters would appear in the axis and its appendages. But the shoot turns out always to be an ordinary leafy branch with the reduced foliage representing the xerophytic adaptation of the group. This shoot is not reversionary in even a barren formal and descriptive sense; for if the fertile scale represents a shoot, now reduced to two ovules and their expanded integuments, the relics of two sporophylls, and if the original development of axis and sporophylls is to be restored, we ought to have in the restoration an axis terminated by sporophylls or by ovules as representing them, since megasporophylls when reduced to a pair are terminal appendages; but this development is not realized in the abnormal cones, in which we find that the shoot arises sometimes above or below the scale, and when in the midst of it, then in the form, not of a stalk, but of a proliferation, upon which the parts of the fertile scale become basal appendages—if they are to be taken as appendages of this shoot at all.

The transformations of the cone are homoeotic. And therefore, while it is in itself not unlikely that the fertile scale represents a pair of sporophylls belonging to an axillary shoot, and while comparative morphology and anatomy may make this view even probable, the monstrous cones, it seems to me, add nothing material to the satisfaction which one may take in this solution of the conundrum.

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[38] CELAKOVSKY'S writings summarize the whole controversy (Abh. Kgl. Böhm. Gesell. Wiss. VI. **11**:1882; VII. **4**:1892; ENGLER'S Bot. Jahrb. **24**:202. 1898). More accessible may be WORSDELL'S review (Annals of Botany **14**:39. 1900), or that of COULTER and CHAMBERLAIN (Gymnosperms 69–77. 1901).

[39] E. g., CELAKOVSKY, Abh. Kgl. Böhm. Gesell. VI. **11**:1882; PARLATORE, Ann. Sci. Bot. IV. **16**:*pl. 13*. 1862; STENZEL, Nov. Act. Nat. Cur. **38**:*pls. 12–15*. 1876; VELENOVSKY, Flora **71**:*pl. 11*. 1888.

Nor is their value improved by the anamorphosis idea. To me at least the "transitions" from fertile scale to axillary shoot do not appeal with the same compulsion with which they appeal to CELAKOVSKY and some others. I can conceive the most perfect of these transitions to represent combinations of historically unrelated form-factors, reproductive on the one hand and vegetative on the other; and in the conception I find nothing incongruous with other facts of homoeosis. If there were originally no shoot in the axil of the fertile leaf (the bract) but only an ovuliferous segment (SACHS-EICHLER) or pair of lobes (DELPINO)—supposing for argument that these notions were admissible on any but teratological evidence—and if by influx of vegetative forces the cone were converted *gradatim* into an ordinary branch, with buds in the axils of the leaves; then it seems to me that we might expect to discover morphogenetic impulses toward the formation of ovuliferous segments and impulses toward bud-formation coexistent and cooperative in the same body of axillary tissue, with such a result as the monstrous cones exhibit. After reviewing the combinations of diverse formative impulses in teratological occurrences generally, I do not feel that CELAKOVSKY's case for the preeminent value of anamorphoses is established. In comparison with other sources of suggestion the monstrous cones seem to have a minimal value. The interest and worth of CELAKOVSKY's thoroughgoing study of the whole subject does not lie in his treatment of monstrosities.

Yet a small degree of approval for the theory which makes the scale represent a shoot bearing sporophylls might possibly be derived from the frequency with which a shoot arises in the site of the scale; and this in spite of the facts that there are irregularities and that more than one plausible reason might be given for the frequent appearance of the shoot. The latter has been found in the genera Larix, Picea, Pinus, Tsuga, Cryptomeria, Cunninghamia, Glyptostrobus, Sequoia, Taxodium, and some other genera.

I hope that it may be clear that the shoot-and-sporophyll theory is not here called in question, but only the use of teratological formations as competent evidence. The ground is taken that these formations do not remove all doubt as to the origin of the fertile scale, but on the contrary only after all doubt has been removed as to the nature of the scale, by legitimate argument from comparison of normal structures, do the monstrous formations begin to have any considerable historical significance.

2. Homoeosis has played a part—necessarily from its nature, which is essentially anarchical, a small part—in the evolution of plants. We can trace to a homoeotic origin certain established sequences in development, of which specific examples may be adduced.

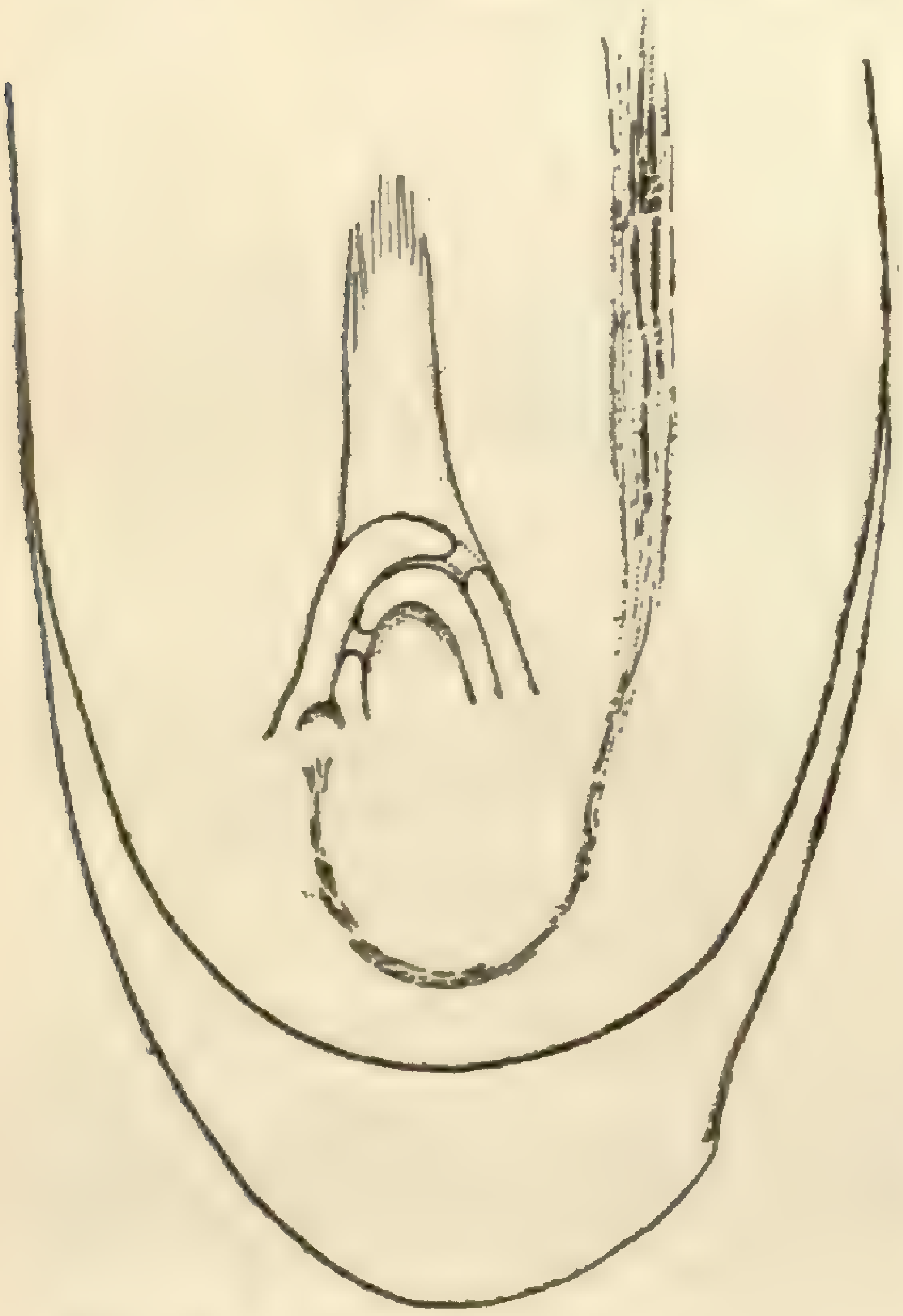

FIG. 16.—Median longitudinal section of root of *Habenaria quinqueseta.*

(*a*) *Habenaria quinqueseta* (or *Michauxii*) of the southern states carries on vegetative reproduction by certain of its roots. At the apex of these roots, close to the *punctum vegetationis,* pointing backward in the embryonic tissues, a stem apex is organized. *Fig. 16* shows its relations to the apical regions of the root. Two leaves and a bud in the axil of one of them have already been differentiated. Subsequently to the stage here represented, the root-apex enlarges and forms at the base of the new shoot a spherical tuberoid growth evidently with storage functions.

As to the evolution of a shoot fundament in this curious position, no one, I suppose, will imagine that the entire evolutionary history of the stem, leaf, and bud in cormophytes has been repeated in the interior of a Habenaria root. It is perfectly clear that the form-giving agencies which shape the leafy shoot in this species have been set to work upon tissues which up to a certain point have been dominated by other forces. There is nothing new except the extraordinary morphogenetic sequence. In this instance, morphic translocation has become habitual, or normal.

(*b*) In *Phyllonoma ruscifolia* of Mexico the flowers are regularly produced from the upper surface of leaves, near the apex (*fig. 17*). There is no adnation in this case, for the anatomy of the blade below the inflorescence and of the petiole shows no addition to the normal vascular structure, indicating any concrescence. Here again an abrogation of ordinary morphogenetic sequence has become fixed in the development.

(*c*) The specific form of the vegetatively derived embryo in some plants must be considered homoeotic; as for example in *Opuntia vulgaris*, described and figured by GANONG.[40] At the time when fertilization should take place, the egg cell, according to GANONG'S observation, has become disorganized. The place of the normal embryo is taken by several embryos budding in from the nucellus. The noteworthy feature of these apogamous individuals is their adoption of the form of the abdicating embryo proper. Here is a homoeosis which has become established and provides a regular means of propagation for the species. A considerable number of such cases is known.

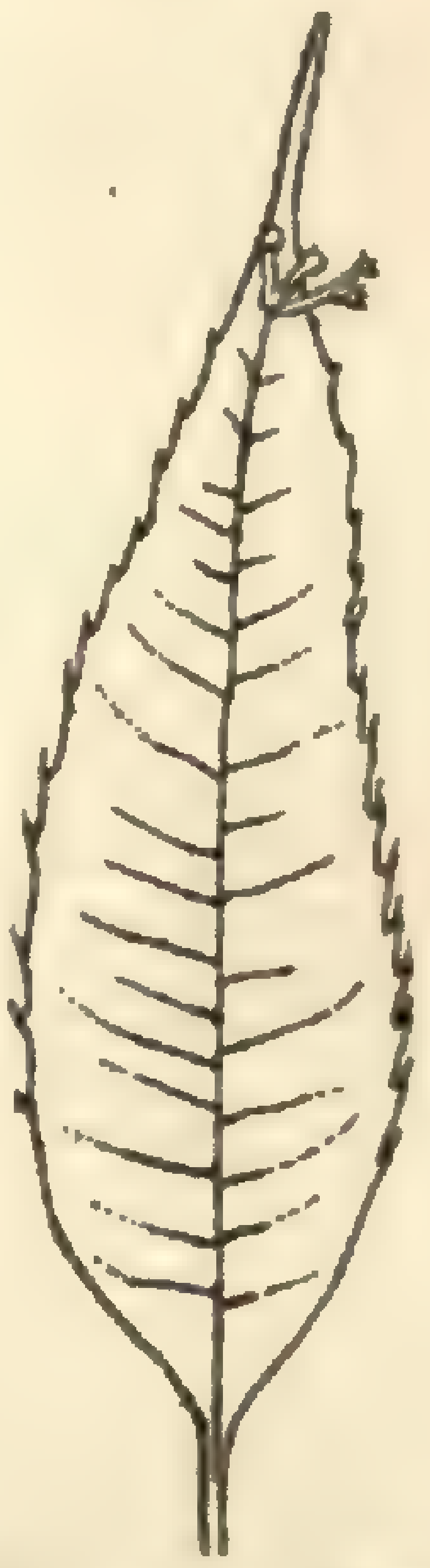
FIG. 17.—Leaf of *Phyllonoma ruscifolia*.

It is natural to imagine that conditions in the embryo sac determine the form of the buds and cause the homoeosis; yet it is not at all certain that such is the explanation of the assumption of form. In a case observed by myself the embryos organize outside of the sac. I refer to *Spiranthes cernua* of the meadows. The upland form of the species has a normal development. In the variety growing everywhere in rich meadows I have seen only polyembryonic seed. Having followed the development with care, I find that the embryo sac ceases to develop after a few nuclei have been formed in it, and is pushed aside by the hypertrophic inner integument. This envelope, normally composed of a few flattened cells overlying the sac, in this variety of the species early takes on a very active growth, forming a mass of cells which, as it comes to maturity, splits up into rounded bodies simulating the embryo of the genus.[41] The formation of embryos is often incomplete and growth then results in amorphous masses; but on the other hand, it is often successful, and gives such seed-contents, consisting of several well-made embryos, as that figured herewith (*fig. 18*). It is true that the form is very simple, for the normal embryo has neither suspensor nor cotyledons. But that cells of the inner integument, ordinarily forming a saccate one-celled layer, with not the remotest resemblance to an embryo, should so much change their habits, and in the transformation should select the fashion, though simple, of embryos, is sufficiently singular. I look upon the process as homoeotic in its nature.

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[40] BOT. GAZETTE 25:221. 1898.

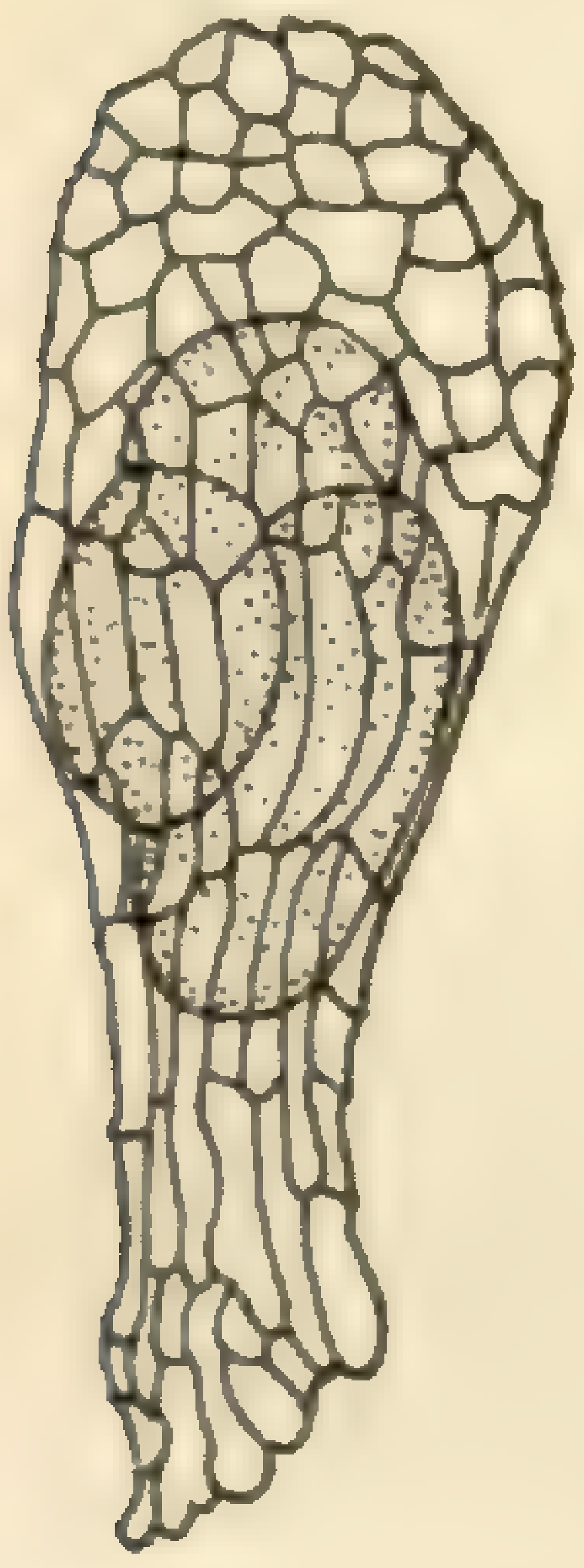

FIG. 18.—Seed of *Spiranthes cernua* (lowland form).

The formation of embryos here is quite independent of pollination, as I have proved by carefully castrated and guarded flowers—an ecologically important item for a species blooming so late in the season. The biological significance of the process, indeed, is—if I may digress for a moment—that the plant by this means combines the certainty of issue which pertains to vegetative methods of reproduction, with the swiftness of dispersal and range of dissemination secured by the seed apparatus. This is doubtless the combination of favorable circumstances which has secured the wide adoption of apogamy in Compositae also. In *Spiranthes cernua*, homoeosis supervening in the integument has doubtless contributed to the abundance of the species in suitable soils from Massachusetts and Ontario to Georgia (I know not how much beyond these limits, which bound my search for the polyembryonic condition).

(*d*) Still more remarkable is the transference, discovered by

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[41] Rhodora 2:227. 1900.

ROSENBERG,[42] of a whole series of characters from the megaspore and embryo sac to a somatic cell in *Hieracium flagellare.* The embryo sac is sometimes formed normally, but in the greatest number of cases this structure aborts. A neighboring cell, which may be situated in the epidermis of the nucellus or in the chalazal region or in the integument, takes upon itself the function of a megaspore, though without reduction of the chromosome number. This cell enlarges to form an embryo sac. Its nucleus divides as that of the megaspore would do; egg apparatus and antipodals are formed; and even polar nuclei fuse to form an endosperm nucleus. The gametophyte is thus reproduced, after the failure of the proper organ to construct it, by a cell of the sporophytic generation. And this homoeotic process is habitual, hereditary, and established in the species.

If HEGELMAIER'S observations upon *Lycopodium Selago* are correct,[43] we may attribute the formation of the gemmae of this species and its near allies to a homoeotic origin. The gemmae—detachable shoots—arise in exactly the position of leaves, from which in their earliest stages they are indistinguishable.

The form of homoeosis most often entering into the diversification of species of plants is apparently that which has above been called entropic. Abscission of leaflets has already been discussed in this connection. Another seemingly homoeotic feature of compound leaves is found in their stipels. An examination of stipels in a considerable number of groups—as in Xanthoxylum, Staphylea, Enscaphis, Turpinia, Robinia, Bradburya, Desmodium, Galactia, Dolicholus, Vigna, Amorpha, Sambucus—strongly suggests that the stipels have arisen as echoes of the antecedent structures, stipules, when in the evolution of the leaf suitable conditions have been established. They occur in plants possessing stipules, and with little doubt already in possession of them before leaf-compounding set in; they are generally useless, as far as one can see; when they have a visible use it is the same as that of the stipules, in a much weakened degree; they follow punctiliously the greatly varying character of the stipules—being large, stout, and thorny; slender, terete, rigid, and sharp-pointed; long, weak, and membranaceous; small or evanescent or flattened and glandular-capitate, etc.—in the different groups; they occur in situations much resembling the situations occupied by the stipules. All of these facts suggest that the compounding of the leaf with organization of partial leaf-stalks, in evolution, has been the occasion for the production of stipels homoeotically.

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[42] Bot. Tidsskrift **28**:150. 1907.

[43] Bot. Zeit. **30**:841. 1872.

Moreover, we may well suspect that in many cases decompounding of the blade has followed upon compounding from the same general cause; the partial blades borrowing the compounding tendency from the parent blade, the whole leaf thus becoming by a single step decompound. The circumstance that the ground-plan of the whole leaf is repeated in miniature in the several parts, in a vast number of decompound leaves of both phanerogams and ferns, and the occurrence of the corresponding type of homoeosis as individual variation in both divisions, lend a color of probability to this conception. Decompounding, on this hypothesis, would have no initial relation to utility, and would not be a product of natural selection.

To consider this matter a little further with respect to ferns: If the variation which we find so frequently in ferns has been the basis of evolutionary advance in complexity of the frond, we should be able to discover in the decompound-leaved species certain relations which would necessarily follow from such an evolution. We should certainly find the ground-plan repeated in the segments. We should expect to find, further, that the historically earlier and simpler conditions would be retained in youthful leaves; and that these youthful leaves would be matched by the segments of the fully developed fronds of the mature plant. Both these expectations are met in many species. Ferns on every hand illustrate the first. Of the second, a single example will be enough to direct attention to the facts which are easily observable. In *fig. 19* are reproduced a youthful frond of *Polystichum angulare proliferum*, and a pinna from an adult leaf. In *Asplenium Filix-foemina* we have a depauperate variety, var. *exile* D. C. Eaton, the mature frond of which is very precisely matched by the pinna of the frond of the typical form.[44]

[44] See EATON'S Ferns of North America *pl. 76*.

Further, if entropic homoeosis has given us decompounding widely in ferns, we shall expect to find species so related to each other that some represent the original types and others the homoeotic derivatives. We shall look for, first, the simply pinnate types; secondly, types in which the pinnae match the fronds of type *1;* and perhaps thirdly, a type in which the fundamental plan is worked out in the pinnules. If the simple type has two modes, as above described for *Polystichum acrostichoides*, we may expect to find either or both represented in the more complex patterns.

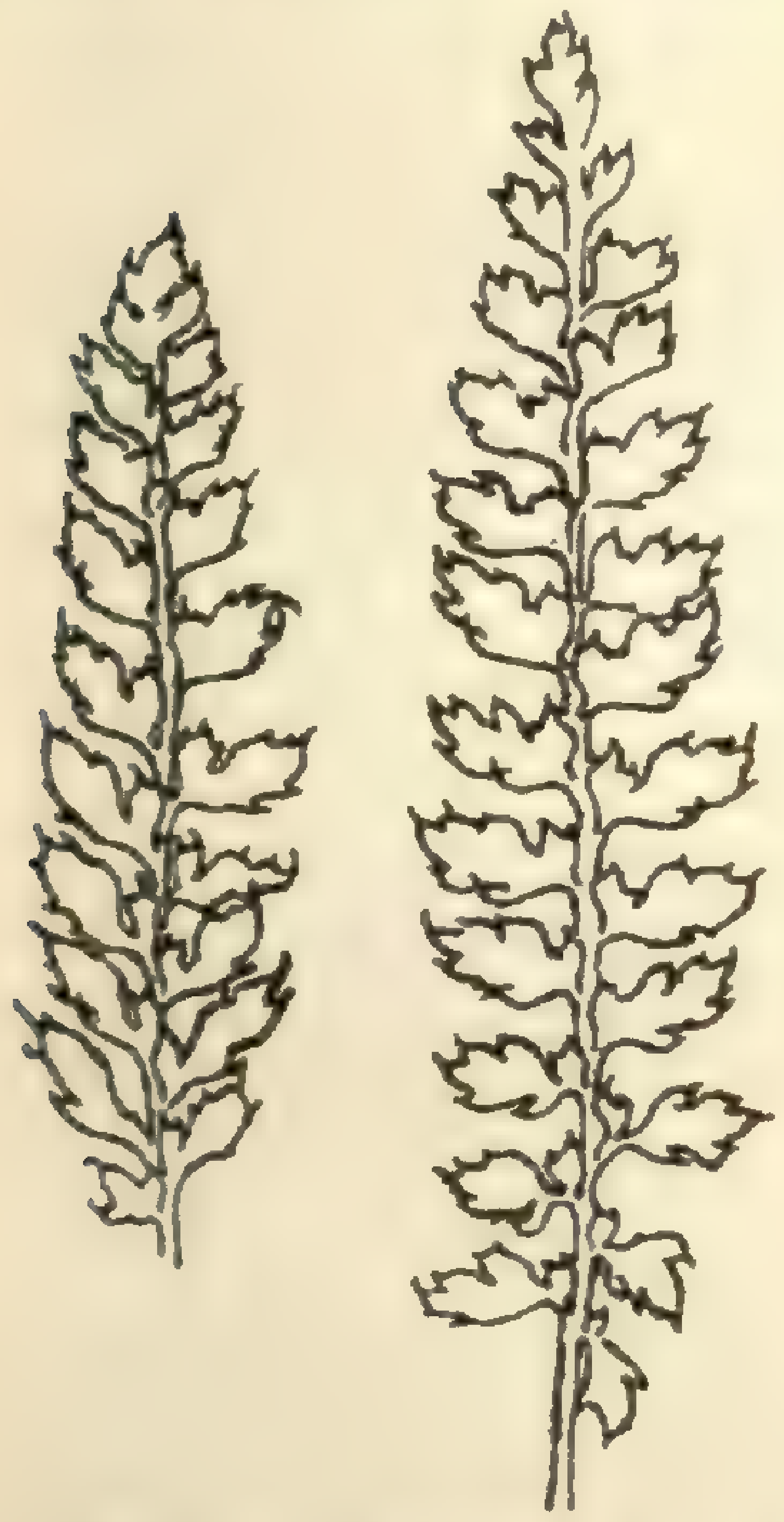

FIG. 19.—Youthful frond and pinna from adult frond of *Polystichum angulare proliferum.*

Anyone having access to a collection of Polystichum may see this projected scheme filled out by existent species. First we have the simply pinnate forms, such as *P. acrostichoides, P. munitum, P. lonchitis;* in which we have two frond patterns, *1a* being the fashion with more or less oblong, non-auriculate pinnae, probably historically earlier, seen in apical regions of sterile fronds; and *2b* being the characteristic plan, the pinnae falcate-auriculate. Then we find many species with pinnae frondescent in facsimile of pattern *1a* or *1b;* as *P. californicum* (*1a*) and *P. Lemmonii* (*1a*), *P. aculeatum* (*1b*), and *P. Braunii* (*fig. 10, 1b*, sometimes *1a*); and others, a considerable number of species. Finally, frondescence of the second degree is well represented in *P. angulare tripinnatum* (*1a*, in the ultimate segments). In *P. scopulinum* the (supposititious) homoeosis is incomplete, the proximal region of the pinnae alone being segmented (*1a*), the distal merely lobed.

We find species so much alike (except that one of two is simply pinnate, the other decompound) that one appears to have been derived directly from the other by entropic homoeosis; as the West Indian *P. viviparum* (decompound *1a*) from *P. triangulum* (compound). In Europe *P. aculeatum* and *P. lonchitis* stand in a similar relation to each other; the slight differences—apart from homoeosis—are such as might be expected to arise in specific isolation.

In homoeosis a character or a system of organization which has been evolved in one part of the body is transferred, ready made, to another part. The great mass of instances are of the class called teratological. By this designation we mean, substantially, that they are suddenly appearing deviations from the customary structure. "Monstrosities" in general have the special value that their chronology is oftentimes ascertainable; we know that such and such identical plants have arisen in the midst of normal relatives. They exhibit, as has been said, discontinuous or saltatory variation. That homoeotic monstrosities typify homoeosis in general, as a saltation phenomenon, may be inferred from the very nature of the process. When, therefore, we discover homoeosis at work in normal evolution, diversifying lines of descent, we are able to augment the steadily increasing collection of evidences for discontinuity in the origin of specific differences.

Homoeotic changes may thus be classed with mutational phenomena. But grouping them with the mutations exhibited by the Oenotheras rests only upon some such negative property as that homoeotic transformations fall outside of any law of the evolution of characters by natural selection. It seems unlikely that the two classes of alterations have anything further in common. Mutation proper seems to result from some qualitative change in the inheritable substratum of organization; while in homoeosis no new qualities are introduced, but only old characters are recombined, or characters are evoked in a new sequence in development. Homoeotic transformations are, indeed, found among the instances of mutation which DE VRIES uses in *Die Mutationstheorie* (for example, peloric *Linaria vulgaris*). They have to be classified under this author's *degressive Artbildung* (p. 461, B 2, a). Yet their inclusion in a classificatory scheme of variations under mutation seems to rest on purely formal and abstract descriptive resemblances.

3. The idea of homoeosis unites for descriptive purposes a great number of facts of ontogenesis which, even though they may not

at the present juncture point a way to the correct mechanical explanation of development, possess in this connection a considerable prospective value. An adequate theory of ontogenesis must take these facts into account.

Their value lies in their exceptionality. Homoeotic occurrences are fundamentally antithetic to our usual conception of the method of development. The most general and fundamental of our notions of a mechanically autonomic evolution from egg to adult, is that of a series of states (A, B, C, D . . . . X, Y, Z), so related that each one necessarily serves as the stage upon which the next state arises. Every one of the several states seems to be the needful condition for the appearance of the next following. This is the primary conception of ontogenesis derived from ordinary experience. It is contradicted by homoeotic formations. We see the usual sequence violated at some point, and a state (as X) arising upon a state (as D) from which it does not normally arise, and from which we have supposed that, in the very nature of the process, it cannot arise directly.

In homoeosis, then, we have a new ontogenetic phenomenon. Herein lies its worth; for every datum of a new sort adds to the materials for a true theory of development, and increases the chances of our finding a clew to the right construction and combination of the materials.

Although the times are doubtless not ripe for the appearance of an adequate theory, and further attempts in this direction may be profitless for the present, yet almost universally there has been felt the desirability of biomechanical hypotheses going behind the bare facts of development. We have had from DARWIN, NÄGELI, DEVRIES, SACHS, ROUX, WEISMANN, DRIESCH, and others a series of more or less elaborate attempts at an explanation. I think that anyone at all familiar with this line of biologic endeavor will recognize the progress in substantial knowledge effected under the influence of such speculations—even though they deal with gemmules, pangens, micellae, biophores, and less concrete "organizations," far beyond the range of the microscope. And it is entirely possible that some of the suggestions already offered may be germinal points from which a verifiable system will develop.

The most persistent attempt at a solution has been made by WEIS-

MANN, who has erected a theory of the nucleocentric type, wherein the control of development is made to reside within the several cells, and specifically within the chromatic matters of the nucleus. Nuclear divisions are conceived as being of two types; namely, (1) equating, in which the germ-plasm is conserved in its integrity, all characters of the mother nucleus being shared equally by the daughter nuclei; and (2) differentiating division, in which the daughter nuclei receive from the parent nucleus unlike assortments of character-giving bodies. All the determinants, capable of giving form to the whole organism, being present in the nucleus of the egg, differentiation is concomitant with an orderly distribution of the governing bodies, effected in the successive nuclear divisions, each different part of the body ultimately receiving its proper kind of determinant.

In view of present limitations of our knowledge, the theory of WEISMANN is a highly speculative system, and as such has been freely modified to meet emergencies arising from the discovery of new facts. There is perhaps little forensic satisfaction to be gained from argument under these conditions. Yet it is undoubted that the the proposal of this hypothesis has prompted investigations leading to interesting discoveries. And even as a means of throwing observations into some sort of order, any such theoretic scheme has its use. It seems to me, therefore, well worth while to consider all kinds of facts of ontogenesis in the light of this and other generalizations in morphogenetics. The facts of regeneration have thus been arrayed with relation to the Roux-Weismann hypothesis. Regenerative phenomena take on, in consequence, some new aspects, and the whole subject gains in spirit. A tentative relation is established between regeneration and morphogenetical theory in general.

The effect upon the Roux-Weismann theory has been the introduction of a fundamental modification. For the power of reproducing lost parts, so widely possessed by animals, and in some degree by plants, is not accounted for by the Roux-Weismann idea in its most unequivocal form. To allow for this faculty, the cells, even of differentiated tissues, instead of being deprived of all elements except those expressed in the usual form of these tissues, are now allowed to retain sets of determinants sufficient for purposes of regeneration. This auxiliary equipment is, however, tightly stowed. Under ordinary conditions only the *differential* determinants are free to influence the development of the cell and its activities, the regenerative or reserve determinants being held strictly under restraint until they are called for, to reconstruct lost members.

Homoeosis has a similar influence with regeneration upon the Roux-Weismann idea; and perhaps a more destructive influence. For while the facts are quite as striking, they are very much more varied and abundant. And if the vast array of data, the existence of which has been suggested in the present article, is added to the evidence from regeneration, the necessity for providing full reserve-funds of determinants in differentiated parts is much increased. Many parts of the body—this statement is made especially with reference to plants—are able to produce almost any other part. We are probably warranted in postulating a pangenerative capacity for every vital member. We know that a single epidermal cell of the leaf in Begonia may originate a complete plant. Indications are not wanting that single living plant cells in general intrinsically possess the same power, ordinarily latent, its exercise inhibited by circumstances. If each cell possesses a complete character-fund, the characters capable of being severally activated upon motion of factors external to the cell, does not the necessity for imaging special individualized determinants disappear? Can we not as well think that differences in cells and forms of organs spring from the nature of the molecule of the form-giving substance (probably chromatin), this substance being the seat of morphogenetic powers ready to be evoked and responding variously to the diverse conditions in which, in the course of development, the substance finds itself placed? Obviously, in proportion as all cells of an organism are made to appear equipotential in a morphogenetic sense, does the need of assuming the existence of different kinds of form-giving substance diminish.

Whatever be the basis assumed for an explanation of the micro-evolution which we call ontogenesis—whether the existence of special form-controlling bodies, or the general properties of the organic molecules, or organ-forming stuffs capable of diffusion, or some other basis—the abrupt diversion of formative currents and transformation of members into others of usually dissimilar origin, the frequent appearance of forms in locations not expected in the ordinary sequence of development, and the potentiality of all parts in each part, indicated by the general phenomenon which we have been calling homoeosis, will need to be provided for in our ultimate theory of development.

STATE NORMAL SCHOOL
TRENTON, N. J.

BRIEFER ARTICLES

LONGEVITY OF SEEDS

In a recent article on longevity of seeds, EWART[1] makes a number of statements which merit comment. He assumes as correct the claim of BERGTHEIL and DAY[2] (working on *Indigofera arrecta*) that they have priority in discovering that the water-resisting power of the seeds of legumes is due to the character of an outer layer of the coat. NOBBE,[3] however, pointed out the fact for *Trifolium pratense* 31 years before the publication by BERGTHEIL and DAY. Both find that stains dissolved in water penetrate in the hard seeds only through the very thin outer layer, called cuticle by NOBBE; but that they do not pass through the palisade layer. This is shown in *fig. 1* of BERGTHEIL and DAY's article. EWART finds the resistance in *Adansonia digitata* to be due to the impermeable nature of all layers of the integument, and I find the same to be true of the hard seed of *Axyris amaranthoides*. It is generally assumed that in the Leguminosae the impermeability to water is never due to oily deposits. I find that the seed of the mesquite (*Prosopis juliflora*) is an exception. By soaking these seeds in ether for several days and then allowing the ether to evaporate, a large percentage is caused to germinate when germinative conditions are supplied, while a direct supply of germinative conditions brings only 5 to 10 per cent. The evaporation of the ether in which they have been steeped always shows an oily residue. Absolute alcohol is less effective in this case.

EWART says: "The seeds of the hawthorn are supposed not to germinate until after a year in the ground. CROCKER obtained no definite confirmation or negation of this fact, but here also it appears to be a case of the slow disintegration of the seed coats." This is hardly consistent with the statement (p. 284) in my paper on the rôle of seed coats.[4] In this case, however, I have underestimated the significance of the coats. I find that in *Crataegus mollis* embryos taken from apples just ripe and entirely freed from the two coats and endosperm begin growth within a few days after being put into the germinator, whether in light or dark. The removal of the inner coat and endosperm is done after sterilization, and the whole process, including germination, is conducted under aseptic conditions. One finds this a very tedious task and the resulting germination is of a peculiar type. In the light the cotyledons begin to expand and turn green. A small percentage of the roots begin growth within a week, but in a larger percentage the roots begin growth only after several weeks and after the cotyledons have expanded to several times their original size. Many of the radicles do not grow even after two months in the germinator. In the dark the growth is similar except that the cotyledons turn yellow and the radicles are even more tardy in their development. The coats then seem to play an important part in the delay, but the tardiness of the radicle in its development is of especial interest and reminds one of the behavior of the fungus-free orchid seeds,[5] or the upper seeds of the cocklebur with coats intact and in 76^{cm} of oxygen pressure.[4] A full investigation of the physiology of the germination of these seeds is now in progress by Mr. W. E. DAVIS and myself.

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[1] EWART, A. L., On the longevity of seeds. Reprint Proc. Roy. Soc. Victoria N. S. **21**. pp. 210. 1908.

[2] BERGTHEIL, C., and DAY, D. L., On cause of "hardness" in seeds of *Indigofera arrecta*. Annals of Botany **21**:57–60. 1907.

[3] NOBBE, F., Handbuch der Samenkunde 117. 1876.

[4] CROCKER, WM., Rôle of seed coats in delayed germination. BOT. GAZETTE **42**:265–291. 1906.

EWART again says: "CROCKER has, however, overlooked the fact that both the early and late seeds of *Xanthium echinatum* will germinate at 20 to 25° C. if the temperature is maintained for fourteen to twenty-one or more days instead of for eight to nine days." I assume that EWART means with coats intact, for that is the connection in which I have made my statement. On November 5, 1908, burs of this species were collected from the plants, the seeds removed from the burs, and the upper seeds soaked 18 hours, so as to show up any defective coats. Upper seeds with perfect coats were placed between wet filters in baths; one maintained at 24–25°, and one at 27–28°. On December 5 none had germinated. Of course with coats removed these seeds germinate within three days, even at 23°. In collections of this species from the crop of 1906 a small percentage of the upper seed with coats intact germinated at 30°. In collections of the crop of 1905, on which the work for my paper was done, the minimum temperature for the germination of these upper seeds lay between 32° and 33° even when they were kept in the germinator for a month. EWART says nothing about the time of gathering, precautions against defective coats, or the percentage germinating at 20–25°. In the absence of all these related data his statement can mean little. In *X. canadense* high temperatures are far less effective in overcoming seed-coat effects, and here a temperature fluctuating between 25° and 41° is most effective. A temperature of 40–43° for a few hours is often more effective than a lower temperature for a much longer period, a fact that led to the discovery of the temperature effects. In the light of this fact, EWART'S statement, "If burs are heated at 40° C. for a day or two, 50° for a few hours during soaking, a variable percentage of the later seeds will germinate within ten days," is not at all new. My data have shown that the effectiveness of high temperatures in overcoming seed-coat effects varies greatly with different species. Further, my data indicate that there is in this respect a slight variation in different crops of the same species gathered from the same locality, and it appears, if EWART'S data have been obtained with proper attention to sources of error, that there is a decided variation in seeds gathered from different regions of the globe.

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[5] BERNARD, N., On the germination of orchids. Roy. Hort. Soc. Rep. 3rd Internat. Congress on Genetics 292–296. 1906.

EWART'S assumption that the coats in the seeds of water plants secure this delay by excluding oxygen does not seem to be true for some of these species. I have mentioned evidence for this in the case of the water hyacinth.[6] One of our students, working with the effects of oxygen on germination, tells me that seeds of *Alisma Plantago* germinate rather readily in entire absence of oxygen, provided the coats are ruptured. In the case of the upper seeds of *X. canadense* she finds that about 3^{cm} of oxygen pressure (0.2 that of the ordinary atmosphere) with two weeks' exposure is necessary to produce germination, even when the coats are removed. These results still need to be thoroughly tested. TAKAHASHI[7] has shown that seeds of rice germinate in entire absence of oxygen. It is probable, therefore, that the coats of the seeds of water plants secure delay in germination mainly by limiting the water supply, as I have pointed out.[6]

Through a discussion of minor and less significant details, however, we must not lose sight of the main conclusion, which is being more firmly established as more data are accumulated,[8] that delayed germination in seeds is generally, though not always, related to seed-coat characters rather than to so-called dormancy of protoplasm. The coat may limit the oxygen supply, as in the cocklebur; it may exclude or merely limit the water supply, as in the seeds of legumes on the one hand and of Iris and other water plants on the other; or it is possible, though not proved, that in some cases it may exclude other chemical compounds necessary for germination.

I believe I am doing EWART no injustice when I say that it is impossible to tell from his paper in how far it is a contribution and in how far a compilation. In this way credit due other investigators appears to belong to EWART, and no one has suffered more in this respect than the writer.—WILLIAM CROCKER, *The University of Chicago.*

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[6] CROCKER, WM., Germination of the seeds of water plants. BOT. GAZETTE **44**: 375-380. 1907.

[7] TAKAHASHI, T., Is germination possible in absence of air? Bull. Coll. Agr. Tokyo **6**: 439-442. 1905.

[8] KLUGH, G. F., Some cases of delayed germination in seeds. Science N. S. **28**: 816. 1908.

RESPIRATION CALORIMETER

On p. 133 of the second edition of Professor W. F. GANONG's admirable *Laboratory course in plant physiology*, which has just appeared, and a copy of which has come into my hands through his courtesy, I am interested to find a Dewar flask figured as a respiration calorimeter. Before my recent paper was published (BOT. GAZETTE **46**:193–202. 1908), I wrote to Mr. GANONG, knowing that he was preparing a second edition of his book, asking him to put my calorimeter into it. He wrote that his book had already gone to press. When my paper appeared he wrote again, saying that he "had been using the Dewar bulbs as a respiration calorimeter some four years past. . . . . Of course the point about the prior use of the bulbs is of no consequence whatever, and I mention it now because of the coincidence in your asking me to mention their use in my book."

So far as priority of use is concerned, it lies obviously with Mr. GANONG. To acknowledge this, and to record another of the curious coincidences which after all are not altogether rare in the history of science, is the purpose of this note.—GEORGE J. PEIRCE, *Leland Stanford Junior University.*

CRATAEGUS IN COLORADO

The attention of the writer has been called by Mr. W. W. EGGLESTON to a misstatement in an article in this journal for November, 1908. On p. 382, line 4, I should have said that the species described resembles most *C. erythropoda*, of the forms known to the writer in northern Colorado.—FRANCIS RAMALEY, *Boulder, Colorado.*

CURRENT LITERATURE

BOOK REVIEWS

The vegetation of Chile

The eighth volume of ENGLER and DRUDE'S *Vegetation der Erde* is a monograph on the vegetation of Chile by Dr. KARL REICHE[1] of the National Museum at Santiago. This is the first volume of the series to deal with American vegetation. REICHE'S long first-hand acquaintance with the Chilean flora makes this contribution a masterpiece, and all the more since fourteen years of effort have been spent with this volume in mind. Chile is to botanists the best-known part of South America, partly by reason of its peculiar accessibility, and partly by reason of the large number of foreign botanists who have made Chile their home, for a time at least. Among those who have contributed largely in recent years, and thus made REICHE'S work more readily possible, are PHILIPPI, JOHOW, NEGER, and DUSÉN. Of particular importance is the work of R. A. PHILIPPI, who was active for over half a century, and who died in 1904 at the age of 96. A short account of botanical investigation in Chile forms the introduction to the work, and there is given a bibliography of Chilean botany comprising 550 titles, of which R. A. PHILIPPI and his son contributed nearly one hundred.

No country in the world presents distribution problems of greater interest than those of Chile, as may be suspected by reason of climatological variation. The vegetation ranges from that of the desert of Atacama in the north, perhaps the driest of all deserts, to the rain forests of the south, where there is a rainfall of 250^{cm} per annum. In northern or tropical Chile (18°–30°) there is the region of desert where there are no marked seasons, and where agriculture is confined to the oases and river banks. In central or subtropical Chile (30°–38°) there are sharply marked dry and wet seasons, and the vegetation varies from steppes northward to sclerophyll forests southward. In southern or temperate Chile (38°–55°) there is a sharp distinction between the very rainy coastal district, where seasonal changes are relatively slight, and the interior, where the climate is dry and where the winters are cold and the summers hot. This rainy coastal strip is characterized by evergreens (temperate rain forest), while there is a strip of deciduous forest (probably the only such forest of consequence in the southern hemisphere) in the drier and periodic climate to the east. It will be noticed that this distribution of forest departs from that given by SCHIMPER in that the deciduous forest lies east rather than south of the evergreens.

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[1] ENGLER, A., UND DRUDE, O., Die Vegetation der Erde. VIII. REICHE, KARL, Grundzüge der Pflanzenverbreitung in Chile. pp. xiv+374. *maps 2. figs. 55. pls. 33.* Leipzig: Wilhelm Englemann. 1907. *M*30.

The second part of the volume presents a detailed account of the most important families of vascular plants and their representatives, the vegetation forms, the formations, and the "biology" of the representative plants. Among the more interesting of the forest trees are the beeches (Nothofagus), of which five species are deciduous and three evergreen, and the conifers (Araucaria and Fitzroya); the latter forms swamp forests, perhaps comparable to our tamarack swamps. These conifers and beeches sometimes form pure forests, but most of the Chilean forests contain many tree species. Other important formations are the bamboo (Chusquea) thickets, xerophytic acacia thickets, and steppes.

The most detailed portion of the volume is that presenting the floristic features of the Chilean vegetation from north to south, and the delimitation of floral provinces. Many endemic species and monotypic genera are found in the country. The final chapters consider the relations of the Chilean flora to other floras (notably those of California, New Zealand, and Argentine), the life-history of the Chilean flora, and the modifications due to human influence. From the developmental standpoint the flora is made up of (1) a tropical contingent, the oldest of all, dating from the Mesozoic; (2) the Andine contingent, a xerophytic element associated with the rise of the Cordilleras; (3) the Californian and Mexican contingent; (4) the Antarctic contingent, mostly in southern Chile, and related to the New Zealand flora; (5) the boreal contingent, perhaps the most interesting of all, there being genera and even species in southern Chile that are common with the far north; (6) ubiquists and littoral pantropists; and (7) adventives. Many admirable plates add much to this important volume.—H. C. COWLES.

The pendulation theory

Now and then a geologist attempts to account for Permian glaciation within the tropics by supposing that the poles have shifted their position during the course of geologic history. Such theories are usually dismissed because they introduce more difficulties than they dispel. A few years ago PAUL REIBISCH, an engineer, laid before the *Verein für Erdkunde* at Dresden such a theory, known as the pendulation theory. There is now presented by Professor SIMROTH[2] of Leipzig a detailed account of the theory, together with a new alignment of facts of distribution. The essence of the pendulation theory is that the earth swings slowly to and fro upon an axis whose poles are in Ecuador and Sumatra. These poles are supposed to remain fixed, but the axial extremities that we commonly call the north and south poles are such for but a moment, speaking geologically. It will be seen that Ecuador and Sumatra must have been in the equatorial realm from the beginning, while for points now on the equator but 90° distant from these fixed poles (i. e. in the French Congo region and in the Pacific Ocean north of Samoa), there may have been in times past any conditions between polar and equatorial. According to this theory, past variations in climate in any given place have been due to pendulation.

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[2] SIMROTH, HEINRICH, Die Pendulationstheorie. pp. xii + 564. *maps 27*. Leipzig: Konrad Grethlein's Verlag.] 1907. *M*12.

Glacial periods, such as the Permian and Pleistocene, have been developed through a poleward swing of regions now temperate; while warm periods, such as the Cretaceous and Eocene, have been developed by means of a swing toward the equator. At the present time Europe and eastern North America are supposed to be swinging southward and getting warmer, while western North America is swinging northward. Pendulation causes constant redistribution in the oceanic waters, by reason of the earth's oblateness, thus accounting for the submergence of coast lines.

The major portion of the volume is devoted to the presentation of the facts of distribution in animals as related to the pendulation theory. It is claimed that the various groups are more or less symmetrically distributed with reference to the fixed poles, owing to the control exerted on migration by the swinging of the earth on its axis of pendulation. One chapter only is given to plants, and in this chapter chief attention is paid to the conifers and Campanulaceae. Three maps are presented, showing the distribution of the conifers. In these and other maps southern Europe figures largely as a center of origin of forms and a center of migration, and the attempt is made to show that migration has taken place symmetrically from that region.

The volume as a whole has a strangely medieval atmosphere. Students of geographic distribution in these days are so accustomed to look carefully for facts that they have largely ceased to care for hypothetical disquisitions such as that of SIMROTH. One feels that the author regards the pendulation theory as a panacea, and that he selects for consideration those facts of distribution which fit it best. Certainly the problems of migration are vastly more than the symmetrical movement of organisms from a center under the control of the direction of pendulation. And the idea of pendulation itself seems more like an iridescent fancy than a reality. Biologists may well wait until there is some astronomic or geologic basis for such a hypothesis before they attempt to readjust their facts to the new theory.—H. C. COWLES.

MINOR NOTICES

Purple bacteria.—A monograph on Rhodobacteria[3] is the natural outcome of the results of shorter studies on the subject which have been presented from time to time by MOLISCH. After a discussion, partly historical, of methods of culture, the author describes eleven new species recognized by him and gives a classification, based upon those of WINOGRADSKY and MIGULA, in which he divides the order Rhodobacteria, containing all known purple bacteria, into two families: those which do and those which do not show sulphur granules in the cell substance. Turning to the biochemical side of the study, MOLISCH examines the relation of these organisms to light, oxygen, and organic substances. With regard to light, the purple bacteria do not ordinarily show positive phototaxis, but are incited to motility which continues for some time after the light is removed. They are not able to obtain carbon from carbon dioxid in the presence of light. Some forms are even anaerobic, and, unlike most pigment bacteria, can produce pigment under this condition. As to the pigment itself, MOLISCH distinguishes two kinds: the red (*bacteriopurpurin*) and a green (*bacteriochlorin*). The latter is distinct from cholorophyll, which fact agrees with that of their inability to use CO_2. MOLISCH concludes that nutrition from organic substance is somewhat related to light and the presence of pigment as shown by the increased energy caused by light; and that thus these forms stand between the colorless bacteria and the green algae.—MARY HEFFERAN.

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[3] MOLISCH, HANS, Die Purpurbacterien nach neuen Untersuchungen. pp. 95. *pls.* 4. Jena: G. Fischer. 1907.

The typhoid-coli group of bacilli.—Numerous methods have been proposed for the ready separation and identification of the typhoid and the colon bacilli in water. Such special media as LÖFFLER'S malachite-green, MACCONKEY'S lactose-bile, ENDO'S lactose-fuchsin, and CONRADI-DRIGALSKY'S crystal-violet, have been more or less successful in the hands of various workers. These are based upon substances which restrain the growth of one type of organism while allowing a characteristic development of the other. DUCAMP[4] proposes for this purpose the use of an "antibacilliary" broth prepared by cultivating in a lactose-peptone solution several strains of *B. coli*, for example, derived from different sources. This broth, when finally filtered germ-free, will be exhausted as a medium for *B. coli*, but will still allow the growth of *B. typhosus*. For the rapid detection of the latter in water, the sample is first plated in phenol broth and inoculations made from the colonies into lactose broth. If a race thus obtained grows in the anticoli and not in the antityphoid broth, and is agglutinated 1:50 by typhoid serum, it is undoubtedly *B. typhosus*.

Studies on the fermentative activities of the typhoid-coli-dysentery group resulted in the confirmation of some facts already known, and brought out some new affinities. *B. para-typhosus*, *B. enteritidis*, *B. psittacosis* Danysz and Thomassen, and hog cholera ferment the same sugars except for two races of hog cholera, which are inactive on xylose, dulcite, and mannose. *B. para-typhosus* Kurth in addition ferments saccharose and raffinose. *B. para-typhosus* A differs with respect to xylose, mannose, and dulcite.—MARY HEFFERAN.

NOTES FOR STUDENTS

Subterranean fungi.—ED. FISCHER has recently made a contribution[5] to the morphology of the fungi. The paper is based on the study of material collected by Dr. W. A. SETCHELL and Dr. N. L. GARDNER in the region of Berkeley, California, during the years 1903–1905. It is of especial interest and importance in view of the fact that so little attention has been given heretofore to the collection of subterranean fungi in North America, and because this new material, some of it in young stages, has enabled the author to put some of the imperfectly described genera of HARKNESS on a better footing, and to revise some of his own opinions as to the systematic position of certain genera which have occupied an unsatisfactory position.

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[4] DUCAMP, LOUIS, Contribution à l'étude de la différentiation du colibacille et du bacille typhique. Action des bacilles du groupe coli-typho-dyssentérique sur les hydrates de carbone. pp. 181. *pl. 1*. Thesis. Lille. 1907.

[5] FISCHER, ED., Zur Morphologie der Hypogaeen. Bot. Zeit. **66**:141–168. *pl. 6*. 1908.

Some of the more important results are as follows: *Myrmecocystis cerebriformis* Harkness and *M. candida* Harkness are shown to be identical, the former being an older and mature stage, while the latter is unripe material of the same species. The former name has precedence. *Myrmecocystis* Harkness (1899) is also shown to be generically identical with *Pseudogenea vallisumbrosae* Bucholtz (1900), and the latter becomes *M. vallisumbrosae* (Bucholtz) E. Fischer. Young material of Piersonia, a genus imperfectly described by HARKNESS from old material, shows that this is a very interesting genus. The small nests of asci in the interior of the fruit body are arranged in separate, pouchlike segments of hymenia, with the free ends of the asci facing open passages or chambers terminating the *venae externae*, the point of junction being rather abruptly narrowed. Paraphyses are irregularly distributed among the asci in groups or partly wanting, but line the surface of the *venae externae*. The latter in the deeper parts of the fruit body are filled with a loose weft of hyaline hyphae developed from the ends of certain of the paraphyses; while toward the external portion of the fruit body brown hyphae are intermingled and become more abundant as the openings of the *venae externae* are reached. In the arrangement and form of the asci Piersonia resembles Pachyphloeus, the absence of hyphae in the hymenia-lined passages recalls Hydnotrya; but the most characteristic feature in which Piersonia differs from other genera is the sharply localized condition of the hymenial parts, since in all other Eutuberineae the *venae externae* are lined throughout by the hymenium. In this respect Piersonia represents a special type at one extreme of an arm in the series Eutuberineae, in which the ascus hymenium has disappeared from a large portion of the *venae externae* and is found only at the innermost terminations of the infolding of the same. FISCHER suggests that Piersonia may give the clue to the proper interpretation of the structure of Choiromyces which he has formerly placed with the Plectascineae, where it certainly occupies a rather anomalous position with its distinct hymenium. His suggestion now is that the large, irregular pouchlike hymenial portions in the fruit body of Choiromyces may, like the smaller ones of Piersonia, stand at the terminations of the *venae externae*, which in Choiromyces have become completely and evenly filled, and all evidence of their communication with the outside may have thus disappeared. FISCHER merely offers this as a suggestion. It will require developmental studies of young material to decide the point. Should this prove to be the true interpretation, it would lend some support to MATTIROLO'S view that the difference between the Plectascales and Tuberales is not fundamentally sufficient to warrant their separation into two groups, although FISCHER has contended, and still maintains, that there is no intermediate type between the two groups; since if his suggestion as to the interpretation of Choiromyces proves to be correct, this anomalous structure would indicate subsequent modification of the *venae externae* and not an ontogenetic connection with the Plectascineae.

Pseudohydnotrya, founded by FISCHER in 1896 on material from California, he now finds is not related to *Hydnotrya* Berk. and Broome, a member of the Eutuberineae, but is generically identical with *Geopora* Harkness, which is closely related to *Hydnocystis* Tul. The fruit body of Hydnocystis possesses a single large hollow space which opens to the outside, though the opening is filled with hairs The wall of the hollow space is clothed with the hymenium. Geopora is a Hydnocystis in which the hymenial walls are deeply infolded in an irregular and complicated manner, in some species closed from the outside, in others communicating in some places with infoldings of the external walls. All recent students of this group agree in placing Hydnocystis among the Pezizaceae, and FISCHER locates Geopora here also, although he formerly placed these two genera among the Balsamiaceae, where they occupied an anomalous position.

One of the very interesting forms proved to be the type of a new genus, *Pseudobalsamia*, which resembles Balsamia in external appearance, but differs in the presence of *venae externae* which open to the outside, thus agreeing with the Eutuberineae. It also differs from Balsamia in the absence of distinct trama plates or veins (*venae internae*), or rather in the masking of them by the irregular distribution of the asci among the tissue elements. In this latter character it resembles the Plectascineae. The *venae externae*, however, are lined with paraphyses, and occasionally asci are found in this layer parallel with the paraphyses. Pseudobalsamia, then, is regarded as one of the Eutuberineae, in which by secondary modification the asci have withdrawn from their regular position in a hymenium and have become intermingled with the elements of the trama, thus simulating one of the characters of the Plectascineae, without showing any ontogenetic connection with that series. This leads FISCHER to regard Hydnobolites, formerly placed by him in the Plectascineae, as one of the Eutuberineae, since the hymenium has probably undergone a similar modification, and the *venae externae* open to the outside. This view of the relationship of these two genera is strengthened by the well-known fact that the asci are often distributed in the trama in certain species of Tuber, as in *T. brumale*, and *T. rufum;* while BUCHOLTZ has shown that in the development of *T. puberulum* the tissue corresponding to the trama areas (*venae internae*) become compressed and changed by the pressure of the developing asci.

The modification which FISCHER'S views on the systematic arrangement of the ascomycetous Hypogeae have undergone as a result of this study are expressed in a résumé. Briefly this is as follows:

1. The *Plectascineae series*, with asci scattered in the tissue of the interior of the fruit body, or in groups, not forming hymenia, includes the two families Elaphomycetaceae and Terfeziaceae. In the latter family remain the genera

Eoterfezia (as a simple form), Terfezia, Tirmania, Terfeziopsis, Picoa (incl. Phaeangium), Delastria, Delastreopsis (as higher differentiated forms). Genabea, Choiromyces, and perhaps also Hydnobolites and Pseudobalsamia are excluded from the Plectascineae, and probably go to the Eutuberineae series.

2. The *Balsamiaceae*, with asci in definite hymenia lining the walls of chambers closed to the outside, includes the single genus Balsamia. Hydnocystis and Geopora go to the Pezizaceae. (See ED. FISCHER, Hedw. **30**:56–60. 1898.)

3. The *Eutuberineae series*, with hymenia lining the walls of interior passages which open to the outside and are either hollow or more or less filled with hyphal wefts (asci rarely withdrawn from hymenia into the trama), includes the gymnocarpic forms and are probably derived from the simpler Helvellales like Rhizina and Sphaerosoma.

Since the second series is represented by the single genus Balsamia, with a hymenium lining interior passages of the fruit body, one is led to inquire if it would not be a more satisfactory arrangement to recognize two series: (1) the Plectascales as outlined above, and (2) the Tuberales, including the Eutuberineae and Balsamia. May it not be possible that Balsamia has been derived from some of the Eutuberineae by a secondary modification of such a nature that the interior passages have become closed from the outside; just as in Geopora, as FISCHER points out, examples occur in which such a secondary modification has probably taken place? The development of Balsamia should be studied with this in view.

Among the basidiomycetous Hypogeae several collections of Hysterangium furnish additional evidence of the existence of a *Hysterangium-Clathraceae series* beginning with Gautieria, and then passing from Hysterangium through Phallogaster, Protubera, etc., to the Clathraceae.

The paper abounds in speculative discussion as to relationship and ontogeny, which is a characteristic of FISCHER'S contributions. In a number of instances his views seem to be based on rather insufficient evidence, which is perhaps the chief adverse criticism which may be made on this contribution. Some of them appear to be well founded, and certainly his present views on the classification of the ascomycetous Hypogeae are to me much more satisfactory than his arrangement in ENGLER & PRANTL'S *Pflanzenfamilien*. It should be said, however, that all his suggestions and speculations are stimulating to thought, and I trust will also stimulate collectors and investigators to bring to the light the riches in subterranean fungi which are awaiting us in this large field of North America.—GEO. F. ATKINSON.

Cytological basis of Mendelism.—GRÉGOIRE[6] has published a critical discussion of current cytological theories, with particular reference to their bearing on the interpretation of Mendelian phenomena. Certain fundamental hypotheses will be mentioned first. His view of the individuality of the chromosomes is based quite largely on his well-known observations, and those of his pupils, on the resting stage of the nucleus compared with the late telophase and early anaphases of mitosis. The attempts of FICK,[7] TELLYESNICZKY,[8] and others to disprove individuality, come in for pointed criticism. GRÉGOIRE concludes that "Il est certain que les chromosomes persistent dans leur individualité, sous la forme de continus structuraux, à travers toute l'ontogénèse." Regarding reduction, he considers it certain that the heterotypic mitosis dissociates the n chromosomes, received by the reproductive mother cells, into two groups of $n/2$; and probable that a paternal chromosome always conjugates with a maternal of the same form. But he finds nothing to *prove* that a pair of allelomorphic characters is fixed only in one pair of chromosomes, nor that the chromosomes conjugated in the heterotypic gemini are homologous maternal and paternal chromosomes.

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[6] GRÉGOIRE, V., Les fondements cytologiques des théories courantes sur l'hérédité Mendélienne. Ann. Soc. Roy. Zool. et Malacol. Belgique **42**:267–320. *figs. 4.* 1907.

The hypotheses necessary to explain Mendelism on a cytological basis are given as follows: (1) The chromosomes play a preponderant rôle in the transmission and determination of hereditary characters. (2) The different chromosomes of a given cell are bearers of different properties. (3) In the chromosomes of a hybrid egg a Mendelizing character is represented only by two chromosomes, one maternal, one paternal. In one of these the character is represented in a recessive condition (modalité recessive), in the other in the dominant condition.

It must be said (and GRÉGOIRE would probably agree with this) that the conception of representative particles in the dominant and recessive condition merely projects the phenomena of dominance back into the germ cell without attempting an analysis of its meaning, or how it comes about, and hence explains nothing. This appears to the reviewer to be a serious and probably fatal objection to the last hypothesis.

On the basis of these hypotheses the germ cells would receive of each pair a single recessive chromosome (maternal or paternal) and a single dominant chromosome (maternal or paternal). In the prophase of the heterotypic mitosis the chromosomes join in pairs, and observation favors the view that these are homologous maternal and paternal chromosomes. Then after reduction half the germ cells would receive a "dominant" chromosome, and half the corresponding "recessive" chromosome. We thus arrive at MENDEL's conception, and the chances of meeting he described between germ cells are here conceived between chromosomes. Granting the three hypotheses then, Mendelian phenomena would be expected to result.

In Pisum eleven or more pairs of allelomorphs have been observed and the reduced number of chromosomes is only seven; which shows that in this case, at least, several characters must reside in one chromosome. The characters must then be confined to separate particles or corpuscles of the chromosomes, and an interchange of homologous particles according to chance during maturation would give the Mendelian combinations. Many observers, including STRASBURGER, ROSENBERG, ALLEN, and SCHREINER, have described such an interchange of particles; but GRÉGOIRE's conclusion, which he has emphasized before, is that nothing in the observations of the nuclear reticulum, the somatic spirem, or the heterotypic spirem justifies the admission of representative particles, chromatic or achromatic. The "chromomeres" observed particularly in the heterotypic spirem, he considers not as autonomous granules imbedded in a substratum, but merely as a substratum impregnated with chromatic material and rather regularly alveolated, giving the appearance of a single or double row of "chromomeres."

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[7] FICK, Betrachtungen über die Chromosomen, ihr Individualität, Reduktion und Vererbung. His-Waldeyer's Archiv. 1906; Vererbungsfragen, Reduktions- und Chromosomenhypothesen, Bastard-Regeln. Engeb. Anat. Ent. 1907.

[8] TELLYESNICZKY, Zur Kritik der Kernstrukturen. Archiv. Mikr. Anat. **60**: 681–706. 1902; Ruhekern und Mitose. *Idem* **66**:367–433. 1905.

GRÉGOIRE further denies that there is an interchange of particles between the parallel filaments in the double spirem stage, such as various cytologists have described. These two facts, namely, the presence of autonomous particles and their free interchange at some time during the reduction processes, would appear to be essential to a cytological basis for Mendelian phenomena.—R. R. GATES.

Extra-floral nectaries and "myrmecophily."—To many who have held the untenable view that plant structures are necessarily useful, extra-floral nectaries have been a stumbling-block. NIEUWENHUIS-UEXKÜLL[9] has made an exhaustive study of the extra-floral nectaries of 100 species of plants growing at Buitenzorg, and it may be said that these studies are of great importance because they show conclusively that we know nothing concerning the advantage of these peculiar organs. There is an admirable critical review of the treatises that consider extra-floral nectaries, beginning with HALL's study in 1762. The term extra-floral nectary was first employed by CASPARY in 1848, who rather inclined toward LIEBIG's theory that they are of value to plants as a means of excreting sugar when present in excess. The classic study of these organs is DELPINO's treatise issued in 1874, in which the term extra-nuptial nectaries is employed, and the idea advanced that the sugar they secrete attracts ants; these insects in turn are supposed to defend such plants against their enemies. Simultaneously with DELPINO, BELT proposed a similar theory for *Acacia sphaerocephala*, and from then until very recently botanists have generally believed in the existence of myrmecophiles, or ant-loving plants. Among the supporters of myrmecophily have been DARWIN, FRITZ MÜLLER, TRELEASE, and SCHIMPER. BONNIER (1878) regarded all nectaries as sugar reservoirs, any other function being thought quite incidental, and KERNER (1878) regarded extra-floral nectaries as protective against "unbidden guests." Beginning with the skeptical attitude taken toward myrmecophily by VON IHERING in 1894, there have been critical contributions by

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[9] NIEUWENHUIS VON UEXKÜLL-GÜLDENBANDT, M., Extraflorale Zuckerausscheidungen und Ameisenschutz. Ann. Jard. Bot. Buit. II. **6**:195–327. 1907.

RETTIG, ULE,[10] and others, all of which are out of harmony with the myrmecophile hypothesis. The work of NIEUWENHUIS-UEXKÜLL confirms these more recent views.

After a detailed account of extra-floral nectaries by plant families, the author summarizes the data presented, and some of the chief conclusions follow. The structure and form of the nectaries do not favor the theory that they originated as adaptations for ant protection; in many cases they specifically oppose such an assumption, and their position on the plant (largely on the leaf undersurface) is such as to be of no purposive significance. The secretions often begin late in life, so that the plant is without protection in youth, when it is most needed. In other cases the secretion begins in early youth and soon ceases, thus leaving the plant for a long time without ant protection, if such exists. The nectaries usually secrete sugar somewhat spasmodically during their period of activity, and are often dry. The nectar of many species is avoided by ants and other animals. The view that the honey-seeking ants drive off crawling insects and other "unbidden guests" that mutilate the flowers, robbing them of honey or pollen, is quite untenable, there being no relation between mutilated flowers, ants, and extra-floral nectaries. Floral mutilation depends on the structure and position of the flower or the weather; furthermore, most mutilated flowers produce as many seeds as flowers that are not mutilated. The honey-seeking ants are not combative and do not attack other insects on the plants they visit; indeed, these other insects often attack and repel the ants. The nectaries, therefore, so far from being beneficial structures developed by natural selection, are harmful to the plants of which they are a part, in that they attract insects of all kinds, which not only eat the sugar but do harm in various ways. Observation showed that individual plants which secreted little or no nectar are less harmed by insects than are those that produce nectar.

This paper, in addition to other recent work, makes it clear that myrmecophily is a figment of the imagination, and the word should be dropped from botanical literature. Ants may "love" plants, but there is no evidence that plants "love" ants. Plants inhabited by these insects, if it seems worth while to group them, may be called myrmecophytes.—H. C. COWLES.

A Mendelian ratio and latency.—SHULL[11] in a suggestive paper makes further contributions to Mendelian theory. In certain bean hybrids three distinct units were shown in earlier papers[12] to be involved, namely, a pigment factor, a blackener, and a mottled pattern. In the last character a peculiar condition is found, namely, the mottled pattern depends upon the presence of a mottling allelomorph in a *heterozygous* condition, the homozygous giving unmottled seeds. This peculiarity results in a new ratio, 18:18:6:6:16, instead of the anticipated 27:9:9:3:16. Latency is held to mean invisibility and not inactivity or dormancy. BATESON's "presence and absence" hypothesis, in which the presence of any character is said to be dominant to its absence, is believed to be of general validity; and his[13] more recent terms "epistatic" and "hypostatic," as applied to the capacity of one unit to hide or be hidden by another, are accepted. Thus in MENDEL's original case, yellow in cotyledons is not to be considered "dominant" over green, but dominant to the absence of yellow and "epistatic" to green, i. e., according to SHULL, causing its "invisibility" but not its "inactivity." This change of view involves some nice distinctions, but appears to obviate some of the difficulties of the older view of dominance, especially in connection with ontogeny. Incidentally all that remains of the Mendelism of MENDEL is his hypothesis of gametic purity. The superstructure erected upon this has grown in complexity with great rapidity.

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[10] See BOT. GAZETTE **44**:314. 1907.

[11] SHULL, GEO. H., A new Mendelian ratio and several types of latency. Amer. Nat. **42**:433–451. 1908.

[12] ———, The significance of latent characters. Science **25**:792. 1907; Some latent characters of a white bean. *Idem* **25**:828. 1907.

With latency thus clearly defined, four types of latency are discussed: (1) "*Latency due to separation*, in which an allelomorph when acting alone has no external manifestation, and is only rendered patent by combining it with another allelomorph." This type of latency is not uncommon, and gives rise to such ratios as 9:3:4, 9:7, 27:9:28. (2) "*Latency due to combination*, in which two dominant allelomorphs, each giving rise to a peculiar character when acting alone, lose their external manifestation when coexisting in the same zygote." This gives the ratio first mentioned above in mottled beans, and may account for certain "mid-races." (3) "*Latency due to hypostasis*, in which the presence of one allelomorph cannot be detected owing to the presence of another allelomorph, the character produced by the latter being unmodified by the activity of the former." For example, a black bean is shown to hide a distinct-brown allelomorph, and a dark orange bean to carry invisibly a light-yellow allelomorph. This condition may give such a ratio as 12:3:1. (4) *Latency due to fluctuation*. Disappearance of characters under unfavorable conditions of nutrition, etc.; a very common phenomenon which may cause discrepancies from the expected ratio. Some of the cases formerly called "incomplete or partial dominance" would probably be classed here. Ratios may also rarely be modified by the failure of certain allelomorphic combinations to form a zygote which will develop.—R. R. GATES.

Respiratory chromogens.—PALLADIN[14] has devised a new, very simple, and effective method of detecting the respiratory chromogens in plants. He uses this method to show the wide distribution of these chromogens in the plant kingdom. In 71 species, ranging from liverworts to dicotyledons, this method showed these chromogens in 67. Their existence in three of the other four species can be demonstrated by other methods. He mentions various fungi that other investigators have shown to contain chromogens, as well as various other higher forms. The points in the literature of this very important subject are briefly and clearly stated.

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[13] BATESON, WILLIAM, Facts limiting the theory of heredity. Science **26**:649–660. 1907.

[14] PALLADIN, W., Die Verbreitung der Atmungschromogene bei den Pflanzen. Ber. Deutsch. Bot. Gesells. **26a**:378–389. 1908.

The same investigator finds[15] that portions of leaves in a 20 to 25 per cent. saccharose solution for seven days show a great increase in respiratory chromogens, over checks immediately taken from the plant, or those kept in distilled water for the same length of time. Illumination during the treatment increases somewhat the chromogen production. If this treatment is continued for 17 days in light, the portions of leaves take on a bright-red color. The color he believes originates from the oxidation of respiratory chromogens. He holds that the sugar greatly increases the respiration and therefore the respiratory chromogens. Whether the chromogen shall become chromatic depends upon whether the oxidases exceed the reductases in activity. In long-continued exposures this seems to occur, hence the red color. He believes that OVERTON's explanation of spring and autumn coloration of leaves is not complete with the consideration of low temperature (as lowering respiration) and abundant supply of sugar as the factors, and considers the relative activity of oxidases and reductases on the chromogen products of respiration as very important.—WILLIAM CROCKER.

Graft hybrids.—WINKLER[16] has begun a series of experiments in the endeavor to produce graft hybrids, such as the well-known *Cytisus Adami* is believed to be. He uses for this purpose certain members of the Solanaceae and Capparidaceae. The method is to graft one species on another in the ordinary manner, and after the scion has "taken," to sever the stem at a point where the tissues of both species will be cut. Adventive shoots then grow out from this cut surface. These will have the characters of either species according to the point they grow from. Shoots arising from the point of contact of the two species gave a peculiar result, which may be described. A scion of *Solanum nigrum* was grafted in this way on a seedling of *S. lycopersicum*, and the shoot in question, originating from the point of contact of the parental tissues, bore leaves having on one side of the stem the characters of *S. nigrum*, and on the other side those of *S. lycopersicum*. In certain cases where leaves were situated on the meeting-line of two kinds of cells, one-half of a leaf showed the characters of either parent. WINKLER proposes to call such organisms, in which one side resembles either parent, "chimeras," and for this plant proposes the name *Chimera Solanum nigrolycopersicum*. He concludes that the cells of two different species may come together in other than a sexual way, and thus serve as the starting-point for an organism which shows simultaneously the characters of both parent species.—R. R. GATES.

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[15] PALLADIN, W., Ueber die Bildung der Atmungschromogene in den Pflanzen. Ber. Deutsch. Bot. Gesells. **26a**: 389–394. 1908.

[16] WINKLER, HANS, Ueber Propfbastarde und pflanzliche Chimären. Ber. Deutsch. Bot. Gesells. **25**: 568–576. *figs. 3*. 1907.

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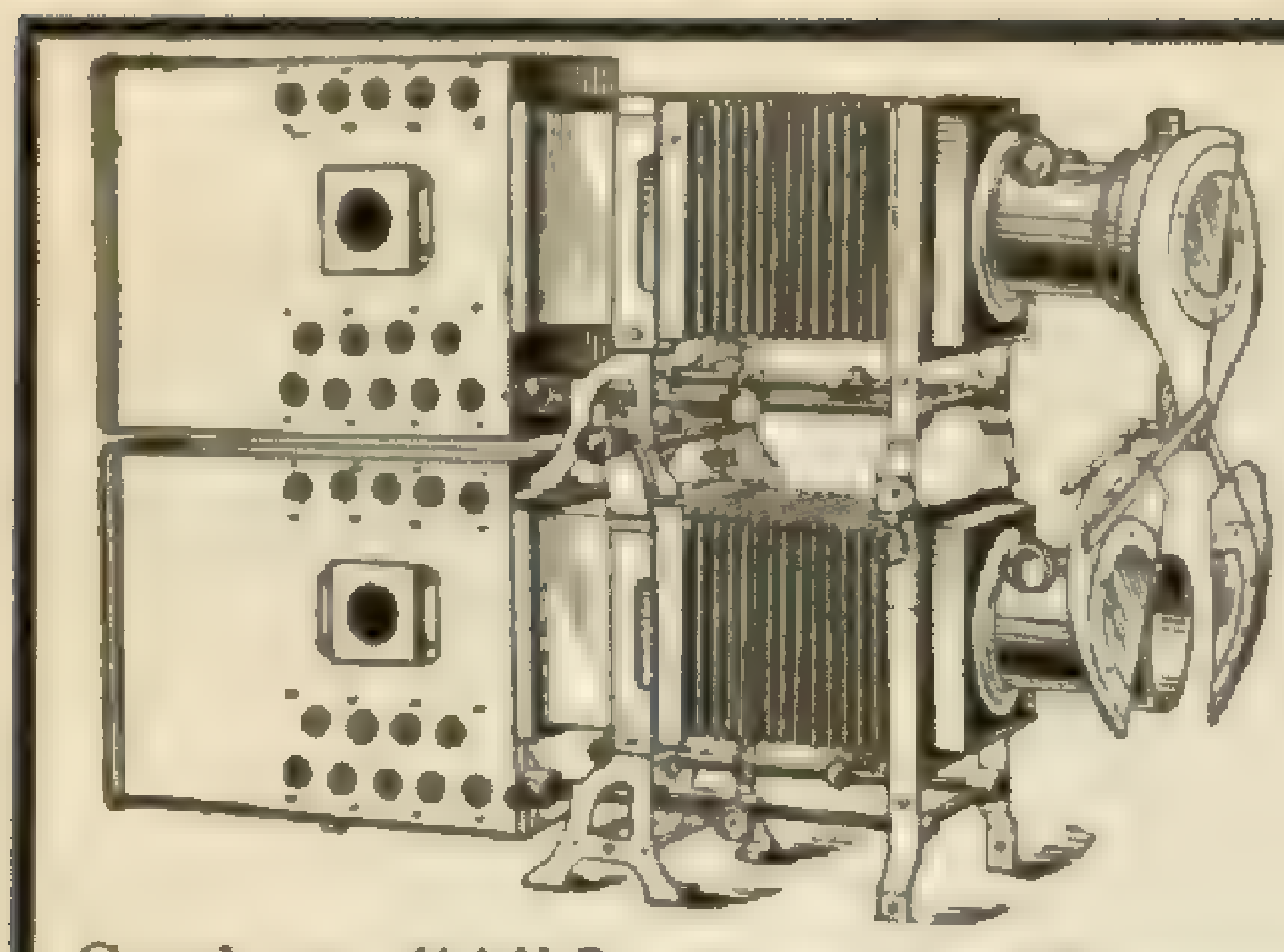

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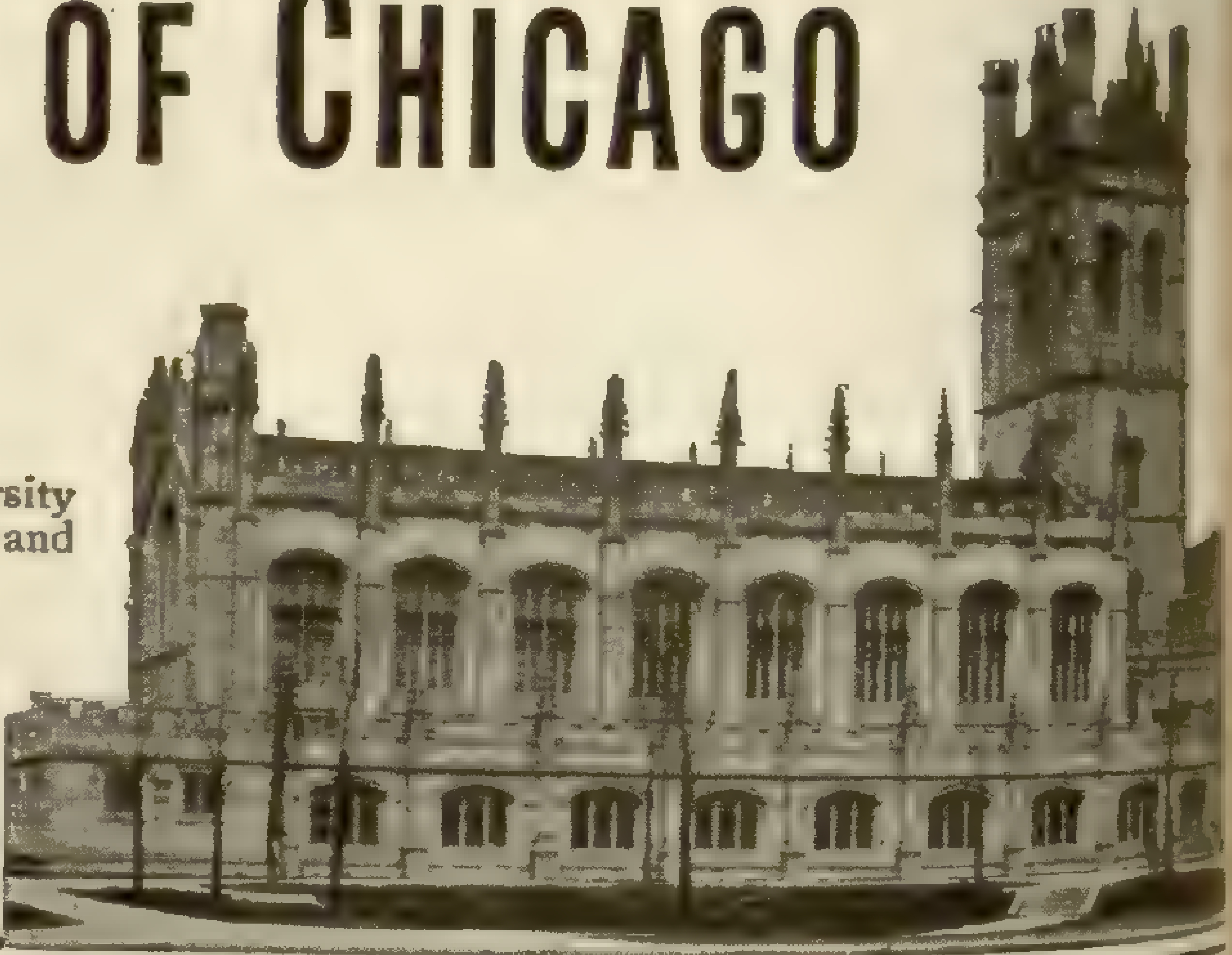

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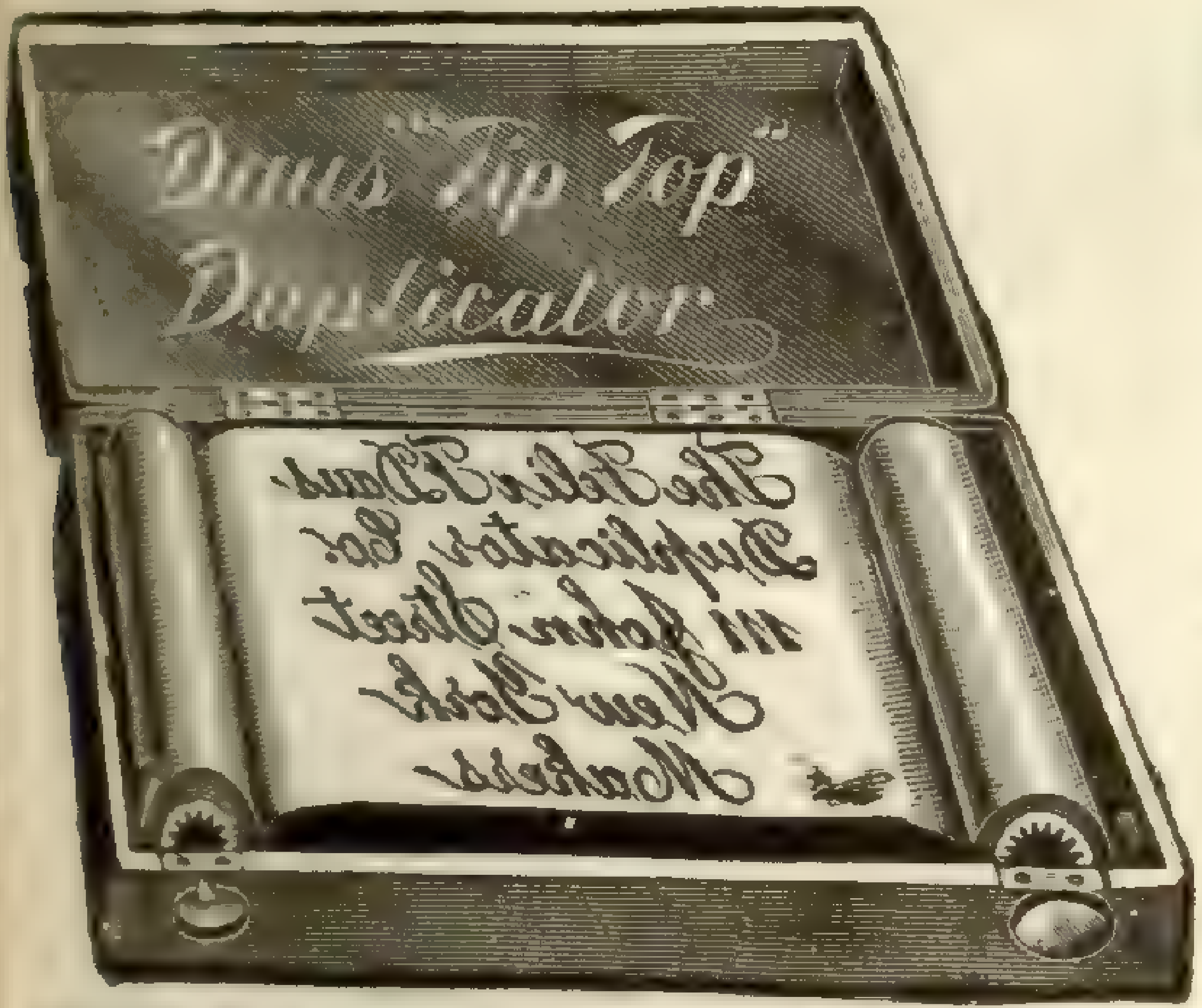

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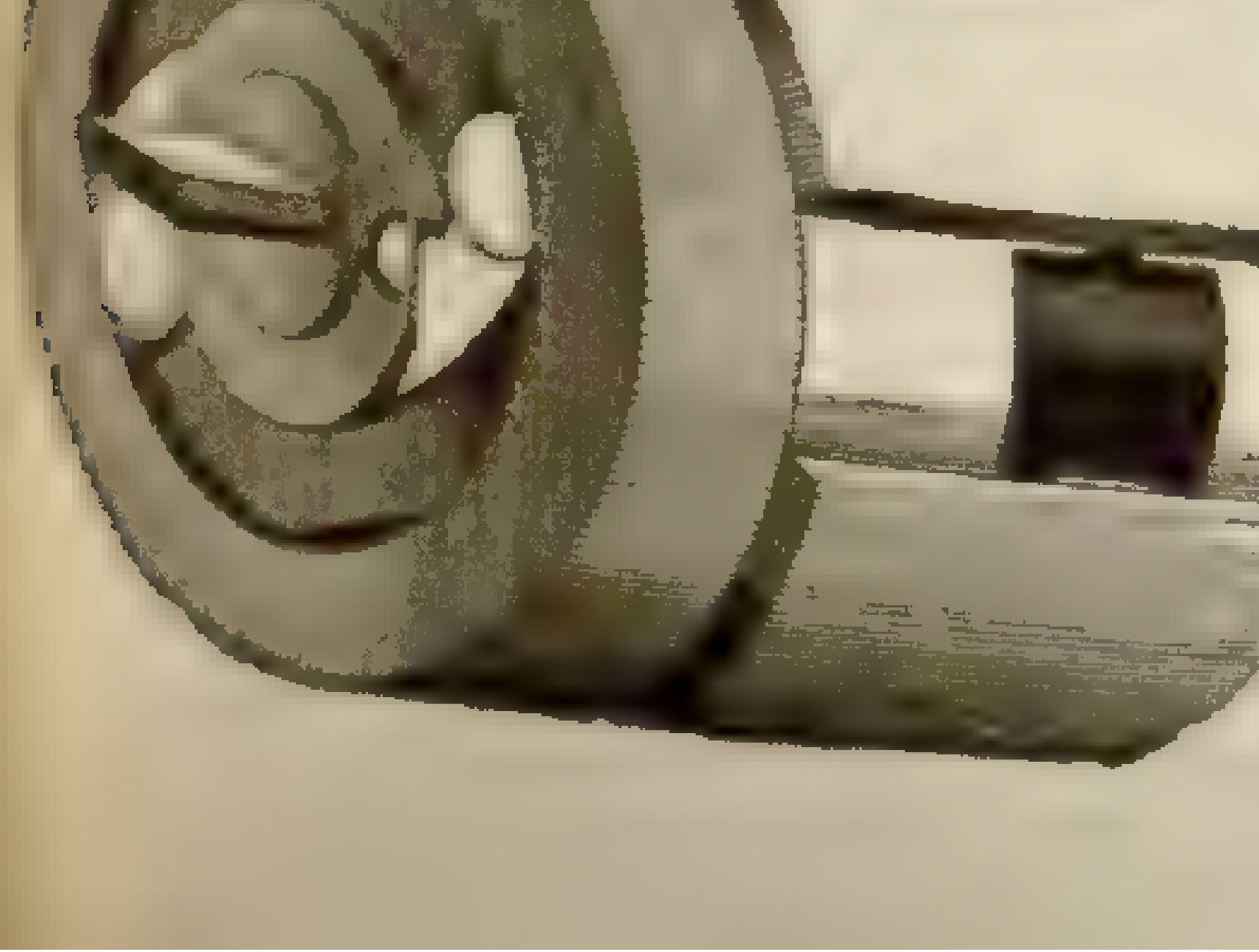

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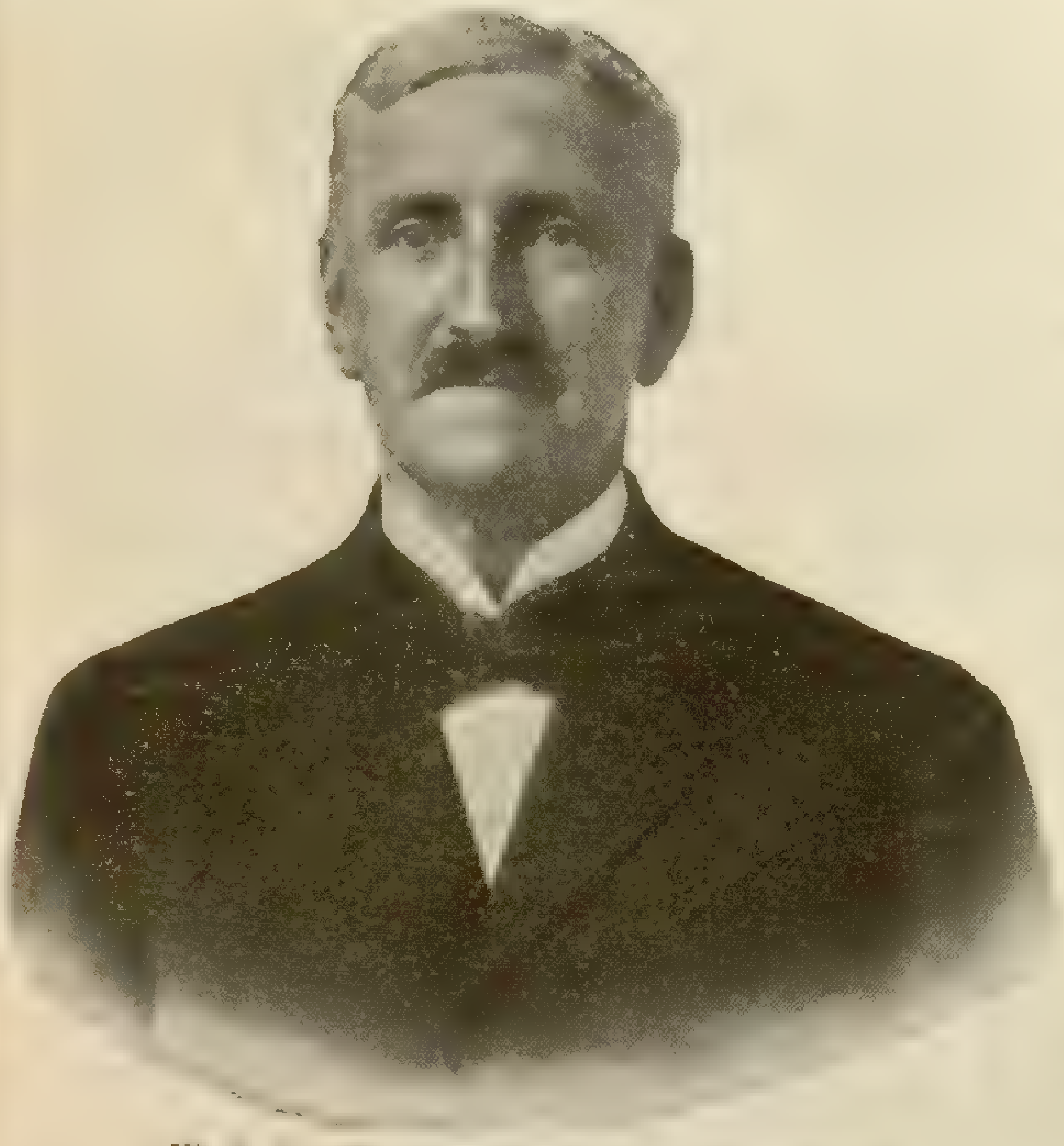

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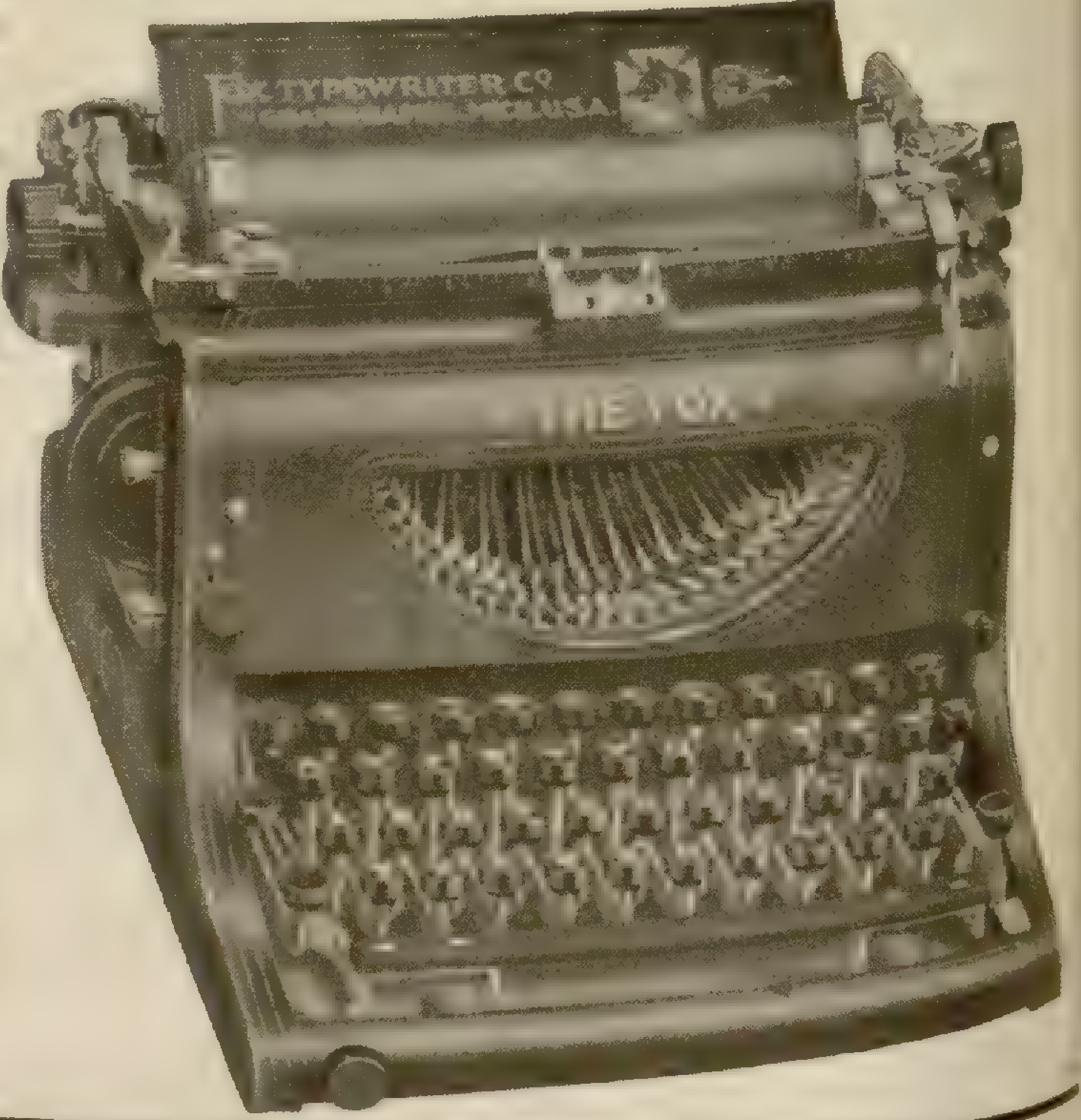

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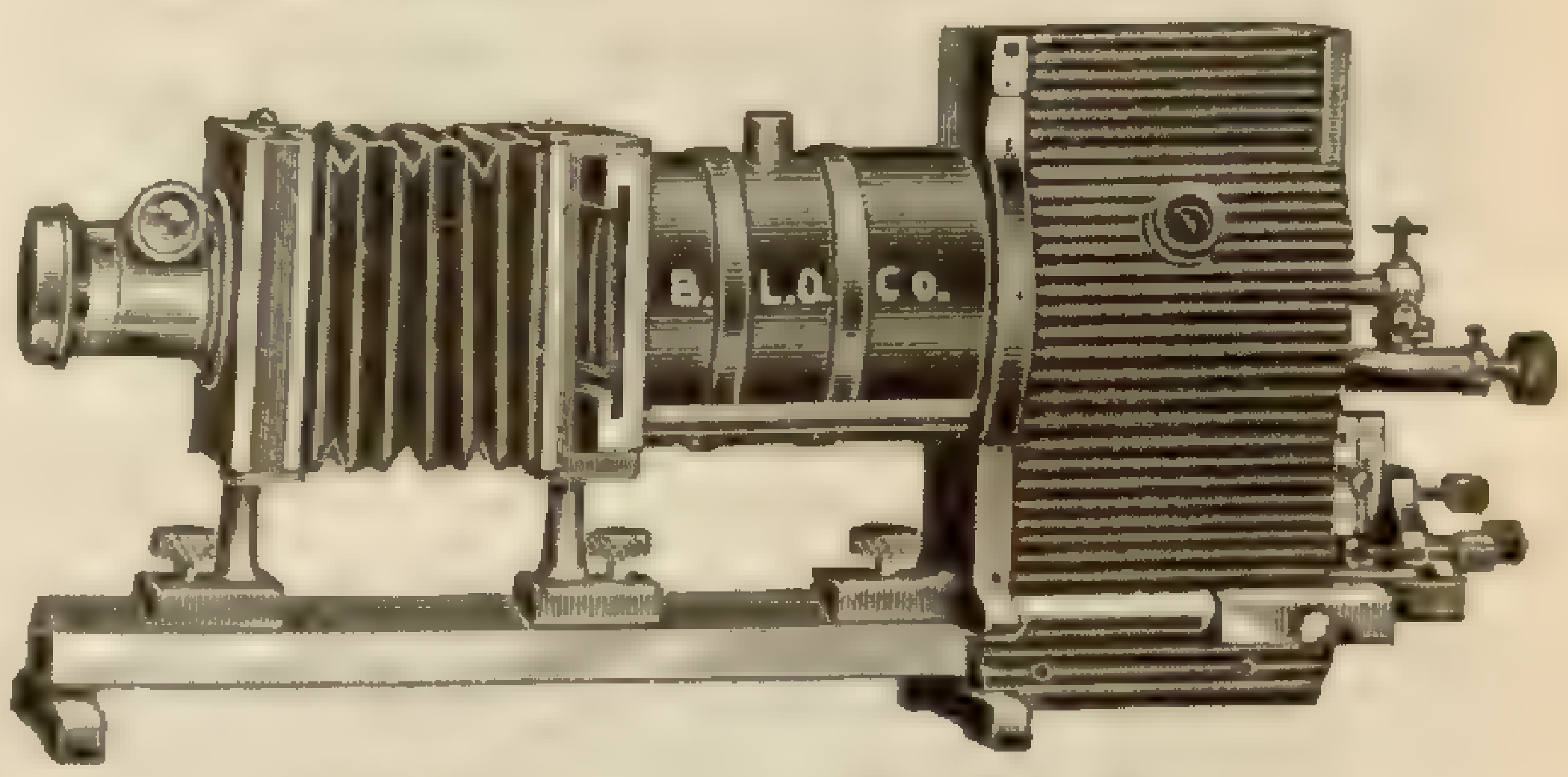

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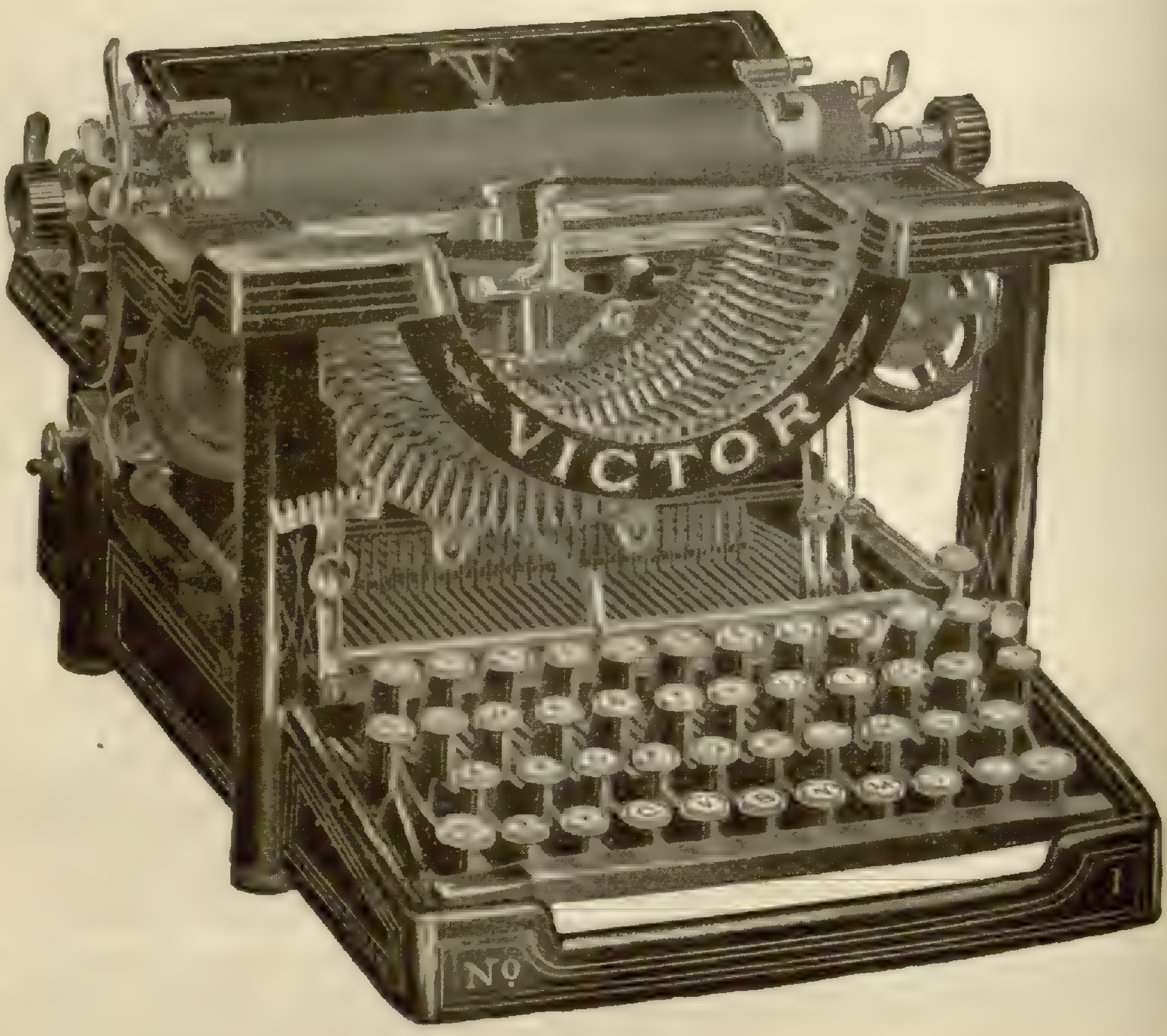

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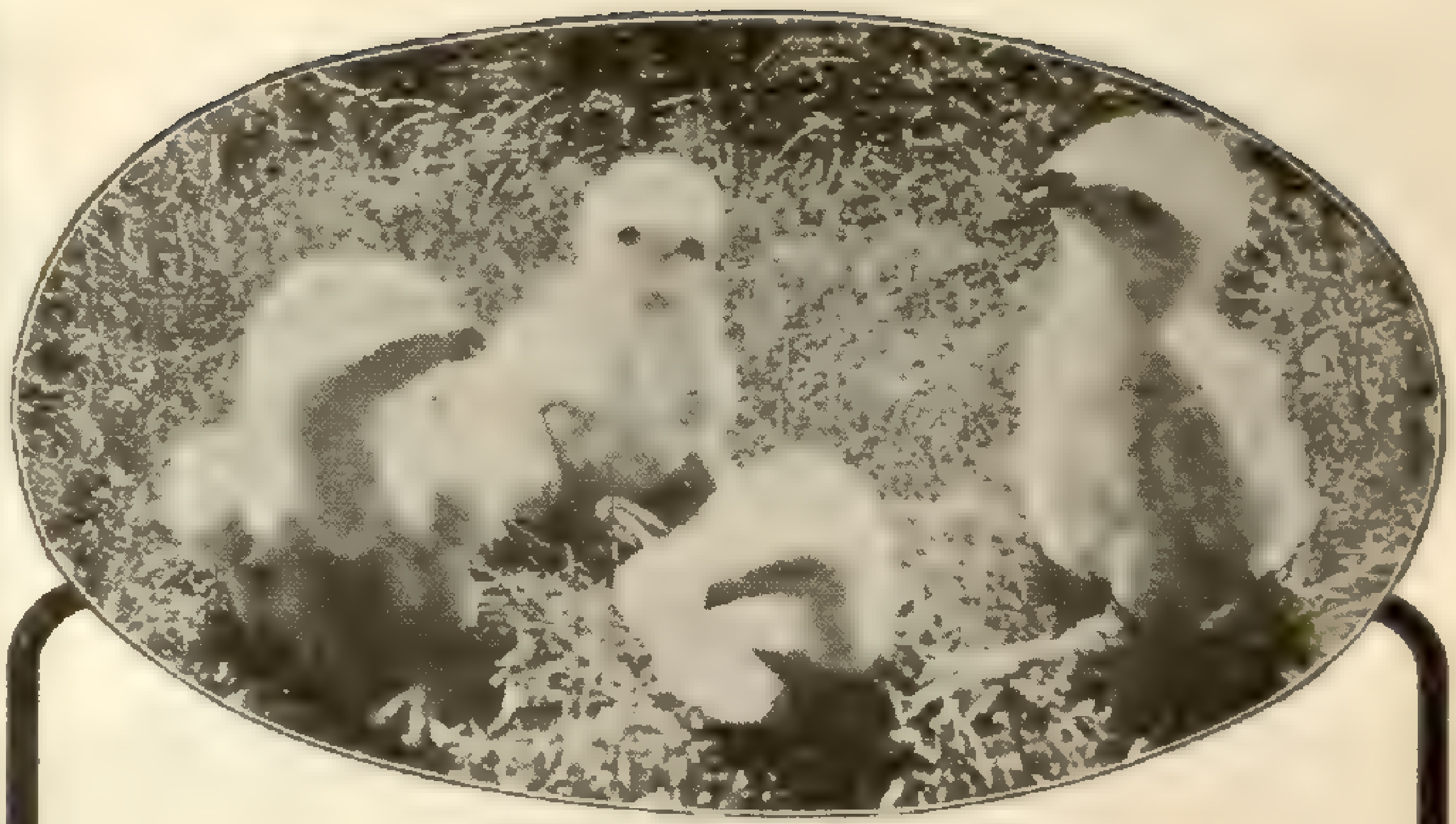

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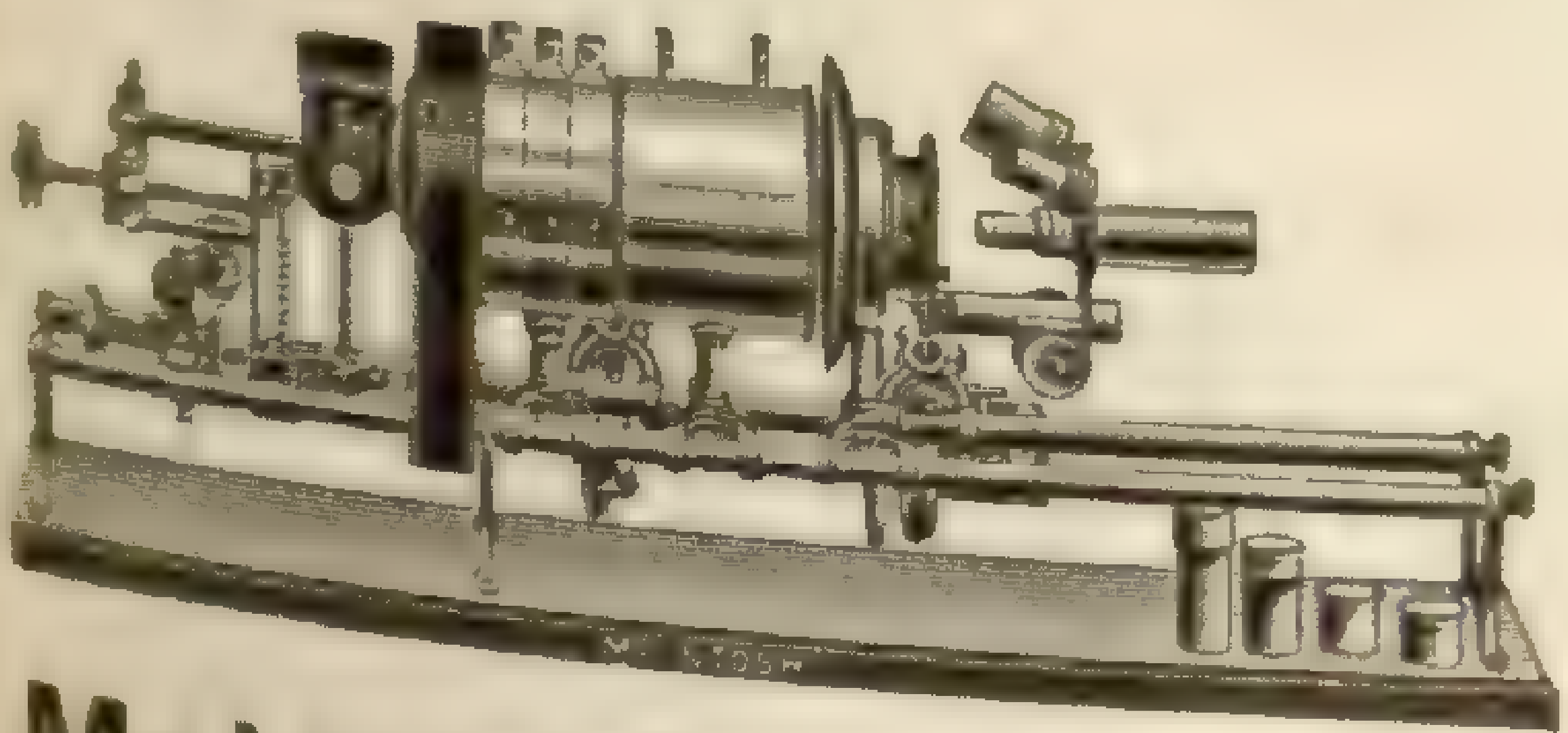

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VOLUME XLVII NUMBER 2

BOTANICAL GAZETTE

FEBRUARY 1909

RELATION OF SOIL AND VEGETATION ON SANDY SEA SHORES

PEHR OLSSON-SEFFER

(WITH TWELVE FIGURES)

The studies on which the present paper is based were carried on during a number of years on a variety of sandy sea shores on the Baltic coasts, in Denmark, Holland, Scotland, and France, on the Mediterranean shores, along the coasts of Australia and New Zealand, in Hawaii, California, Mexico, and Central America.

In this paper I propose to give some of the observations made by myself regarding the conditions for plant life on coastal sand formations, and also to compare these investigations with the accumulated results from studies on this subject obtained by others.

Although considerable attention has been given to some of the most important points, I have as yet not been able to study in detail others, equally weighty; and in trying to interpret several of the phenomena of the distribution of sand vegetation I have found myself confronted with many problems, for the solution of which there is but little definite evidence at hand.

In discussing the factors that influence plant life, I have found it convenient to classify them into the following groups: atmospheric, hydrodynamic, edaphic, topographic, and historical factors.

To atmospheric factors all those are here referred, which directly influence the vegetation through the air. The atmospheric temperature, the light conditions, the variations in air moisture, the movements in the atmosphere, and the electricity are the principal factors of this kind. As hydrodynamic factors I understand all those connected with the water content of the substratum, and edaphic factors are those relating to the chemical and physical quality of the soil. I call topographic those factors which have reference to the external features of the ground, and they affect indirectly more or less the factors belonging to previous groups. Historical factors are those which in the course of time exert an influence on the topography and thus indirectly on the plant covering.

Another series of factors analogous to the physical factors influencing plant life are the biotic. They are either zoobiotic or phytobiotic. Of the former especially the influence of man has to be recognized in connection with the study of vegetation on coastal sands. The phytobiotic factors are those caused by the plants themselves, and the mutual relationship of sand plants will be discussed in another paper.

Atmospheric factors

It is impossible to determine the relative importance of different factors influencing plant life, or to give one of these factors precedence in rank before another, because this depends in different cases on different conditions. It may be said, however, that the whole group of atmospheric factors is the most important, especially because of their influence on the transpiration of the plants. Sand vegetation is particularly affected by: (1) the large amount of heat absorbed by the sandy ground and reflected from its surface; (2) the intensity of illumination, both direct on the open, unprotected formation, and reflected from the white sand; (3) the exposure to winds, which constantly change the atmosphere.

TEMPERATURE.—If we compare in a general way the temperature conditions in a few of the localities under consideration, we find that there is no significant difference in results as regards development of sand formations or their vegetation in cold and warm countries. On the dunes along the Gulf of Finland, where the vegetation is in a dormant state for at least three months of the year, the sand drifts best during winter, when the grains are covered with a thin surface of ice and are smooth. The friction is less and they are able to move slowly forward. The herbaceous vegetation is absent at this time, and the deciduous shrubs are without leaves. There is consequently nothing to arrest the movement of the sand.

On the Queensland coast, with a semitropical climate, the vegetation period extends over the whole year, but the sand drifts here much better during the summer, because winter is the rainy season, and when wet the coherence of the sand is greater. Plants like Ammophila, Cakile, Salsola, and Atriplex, of which the parts above ground die every winter on the Baltic coasts, grow all the year round on the shores of Australia, and there is no difference, external or internal, in structure. *Convolvulus soldanella* on the coast of Holland does not differ from the same species on the shores of tropical countries, where it is common (*fig. 10*).

Dunes are formed in warm countries more generally than in cold because of the longer periods of drought, which favor the drifting of the sand. We refer to the enormous areas of sand formations in Africa, both on the coasts and in the interior, in the deserts of Asia, on the coasts of India and Australia, in the interior of the latter continent, on numerous tropical coasts as Java, Hawaii, etc. The dunes which occur in really cold countries, as in certain parts of the United States and northern Europe, are insignificant in comparison with the former.

It would be of considerable interest to have correct data of temperature conditions from the various localities where the author has made his studies of the coastal sands. The field-work on which this paper is based, however, has been conducted for comparatively short periods at each place, and the temperature observations made do not offer, therefore, any reliable basis for comparisons. Official data, obtained from meteorological stations on the coasts, are also unsatisfactory for our special purpose, because the instruments usually are kept close to buildings, away from vegetation, in more or less sheltered positions, and because of these facts the observations cannot serve for any definite conclusions as to the real temperature conditions under which the vegetation has developed. It is not necessary to burden these pages with computations of any general data of the kind referred to. The author has compared a great number of temperature statistics from different coasts, but he has entirely failed to find any apparent rules applicable to the development in general of sand vegetation in different climates. This negative result is not due to absence of such laws, which certainly must exist. It merely shows that our knowledge is deficient and the present method of taking temperatures at meteorological stations is entirely inapplicable to the subject under consideration.

For ecological purposes temperature observations in the field have to be made very carefully if we are to draw from them any conclusions of value as to the influence of heat on the vegetation. And further, they have to be extended over a long period of years before we are justified in advancing any general laws of temperature influence on distribution of plants.

Let us here draw attention to the opinion held on this question by the greatest authority on ecology, Professor WARMING. In his renowned handbook on ecological phytogeography (**14**) he says on page 22, speaking of the many attempts to determine the sum-totals of temperature in relation to geographical distribution, that these investigations need in a very high degree to be supported by really scientific experimental determinations of the cardinal temperatures for the phenomena of different species. And even the results of such observations would hardly be sufficient for the solution of the very difficult and complicated questions of the importance of heat conditions for distribution of species and phenological phenomena, as other factors, perhaps, to some extent can replace a higher temperature.

One feature of the heat conditions on coastal sands is apparent. That is the great fluctuation of diurnal temperatures. On account of the low specific heat of sandy soil, the surface layers are rapidly heated by the sun in daytime and as quickly cooled by night. These variations of temperature are conducted by radiation to the lower strata of the atmosphere, or those in direct touch with the plants, which consequently are greatly affected by such changes.

Of some occasional observations by the writer on the diurnal range of temperature on sand dunes the following may be mentioned as examples of the great divergence between temperature extremes in such localities.

Observation 64.—Dunes at Hangö, Finland, September 10, 1897. Maximum temperature in the shade (thermometer from unknown maker) 28°8 C., between 6 A. M. and 6 P. M Minimum (thermometer from WALLMANN in Stockholm) 2°6 between 6 P. M. and 6 A. M. Range 25°6. The instruments were placed on an open sand surface 25^{cm} above the ground, and were shaded by white canvas, 2^{m} high. Ordinary thermometer readings in the shade were taken every hour in the daytime, giving the following results:

6 A. M.	8°5 C.	10 A. M.	14° C.	2 P. M.	23°6 C.
7 A. M.	9.2	11 A. M.	17	3 P. M.	27.2
8 A. M.	9.8	12 M.	19.4	4 P. M.	27.5
9 A. M.	11.4	1 P. M.	20.6	5 P. M.	22.4
				6 P. M.	15.9

This place of observation was on an open spot, unprotected from the winds. About 60^{m} inland between the pines, and sheltered from winds, the thermometer gave 7°4 C. at 6 A. M., 9°2 C. at 9 A. M., 16°6 C. at noon, 28° C. at 3 P. M., 16°2 C. at 6 P. M. This shows that the temperature was slower to rise in the morning and forenoon, but once high it was also slower to decrease, when the energy of the solar rays was diminishing toward evening.

Observation 576.—Dunes at North Beach, near Perth, Western Australia, September 12, 1902. Maximum in the shade 31°1 C. (8 A. M.–6 P. M.). Minimum 6°8 C. (6 P. M.–8 A. M.). Range 24°3. The instruments, from Negretti & Zambra in London, were elevated 30^{cm} above ground and shaded by a white canvas tent with open sides. The hourly variation was the following:

8 A. M.	7°9 C.	12 M.	23°6 C.	4 P. M.	19°5 C.
9 A. M.	11.2	1 P. M.	29.4	5 P. M.	16.3
10 A. M.	15.6	2 P. M.	30.7	6 P. M.	9.6
11 A. M.	18.6	3 P. M.	20.3		

These data show, as in the previous observation, that the temperature rose steadily until about 2 P. M., although the rise is so much more rapid in these latitudes on account of the greater energy of the sun. In this case, however, over 10° in a single hour, and nearly 10° more between 4 and 6 P. M.

On the coast of Western Australia a sea breeze always sets in about noon, according to Cooke (4), the temperature then begins to fall until evening, and the nights are generally cool the whole year round.

The influence on vegetation of such a wide range of temperatures must necessarily be of considerable importance. Although these air temperatures have been largely affected by radiation, the direct radiant heat of the sun is still more important. Actinometric methods of registering intensity of solar radiation are, as yet, very unsatisfactory. Almost the only instrument available for field observations is the so-called black-bulb thermometer *in vacuo*. The rather casual observations of this kind made by the writer will be referred to in another place in connection with some transpiration phenomena. It may suffice, however, to say here that these occasionally taken measurements, in spite of their discontinuity, have convinced the writer that the surest and most effective way of attacking the problems of heat influence on vegetation is to pursue investigations on the lines of actinometric records. Neither the mean temperature of the air nor the sum-total of atmospheric temperature is of such importance to vegetation as the amount of direct solar radiation and radiation of heat from the ground. The value of the former factor in climatology has long been recognized by meteorologists.

We must never lose sight of the fact, however, that it is not one factor alone that determines the development and distribution of the vegetation, but a resultant of the many different conditions to which the plants are subjected. This has been duly emphasized by WARMING (**14**).

LIGHT.—In the closest relation to atmospheric temperature, and especially to radiation of heat, is the factor of light. The intensity of illumination is remarkably large on the open sand formations of the coast, and this circumstance is noticeable in the many protective adaptations of plant structures against the influence of light. There are as yet no reliable means of ascertaining the intensity of the light, and we have consequently no basis for comparisons on this subject. The strong insolation on the white surface of the sand favors a greater variation of temperatures than on other formations of the coast. The radiation is, however, generally less on the coast than in localities far away from the sea because the larger quantity of aqueous vapor in the atmosphere in the former place tends to check this terrestrial radiation.

HYDROMETEORIC CONDITIONS.—This term has here been used to distinguish the factors of atmospheric humidity from those of the water content of the soil or the substratum from which the plants take their supply. On coastal sands it is perhaps more apparent than on other formations that there is some difference in influence and effect on vegetation of the moisture contained in the air and of the water in the soil. It is, however, always extremely difficult to decide to what extent certain adaptations are due to one factor more than to another, especially when we do not possess detailed observations.

AIR MOISTURE AND EVAPORATION CAPACITY.—The supply of atmospheric moisture is to a great extent obtained from the ocean, and it follows that on the coast the amount of humidity must be much greater than farther inland. This is in fact an everyday observation.

We do not know for certain to what extent the plant is able to condense water vapor and absorb atmospheric humidity, but we do know that moisture in the air greatly lessens transpiration, and, other factors being equal, transpiration ought therefore to be less on sea shores than inland. Now it is not the absolute humidity that determines the amount of evaporation, but the saturation deficit or the amount of water which the atmosphere at a certain temperature is able to absorb (WARMING). In the continental interiors the evaporating power of the climate is very great during summer, and on account of the cold quite inconsiderable during winter (HANN **7**). If we compare the habits of certain plants which occur both in the interior deserts, and on coastal sands we shall find them instructive. For instance *Mesembryanthemum aequilaterale* has the same appearance when growing on the beach or in the immediate neighborhood thereof, as when occurring on the interior sands of Australia, many hundreds of miles from the coast. But when found at a certain distance, 0.5^{km} or so, from the beach, *outside the influence of the spray from the sea, and sheltered from the full force of the ocean*, it grows higher, its leaves are two or three times as long, and its succulence is less marked than in specimens from the beach or from the interior. In the case of the writer's observation, the places of growth were as nearly similar as possible with regard to exposure to the rays of the sun and moisture in the soil. Some notable differences in anatomical characters observed in this connection will be alluded to in another paper. These characters also proved that the devices for protection against excessive transpiration were not so well developed in the specimens which were not exposed to the strong salt-laden winds, although they had the full benefit of the coastal moisture.

If we may be allowed to draw any inferences from this fact, we should conclude that, as a rule, *transpiration is less on coastal than on interior sands*. There are other factors, however, to be taken into consideration, which somewhat equalize the conditions, as the wind and the salinity of the atmospheric moisture.

Everywhere on warm coasts, especially in the neighborhood of the sea, on the beach, we can notice a peculiar sand flora. It is characterized by species which do not occur farther inland, and on the other hand inland plants as a rule do not go down to the beach. The greatest part of this strand flora consists of halophytes or plants growing in salty situations.

It is generally assumed that the conditions in which halophytes thrive are dependent on the amount of salt present in the soil. As we shall show, when speaking of the edaphic factors, the quantity of salt present in the soil in some of the coast formations is quite inconsiderable, but still the plants exhibit the same characters typical of those which grow where salt occurs in the soil.

We cannot here escape the conclusion that the influence which is exerted on the plants in one case by the salt-water content in the soil, in the other case is brought about by some other cause of similar kind.

Analysis of spray from the sea reveals the presence of a large amount of salt, usually even more than in the sea water, because water is evaporating from the drops of spray and the fine particles of moisture near the ocean. This salinity of the spray is greater at a high temperature, as the evaporation is then more intense, and it is common to find on hot days, with sea wind carrying moisture landward, that salt is deposited in form of crystals on the plants and on other objects, as well as on the ground.

A few analyses will be given to illustrate this large quantity of salt in the atmosphere on the sea coast. In all instances when samples of spray were secured, the method was as follows. Pieces of muslin, thoroughly examined and found free from salts, were dried and kept in tight-closed jars until exposed at the place were the sample was to be taken. The muslin was then exposed to the sea spray; the temperature and time of exposure were registered, the muslin bottled, and later examined in the laboratory. At the same time samples of the sea water were secured for chemical analysis. The following results were obtained from four observations:

I. Nagu, Högsar, Finland, August 22, 1897. Atmospheric temperature 19°.5 C. Sky clear. Velocity of wind about 7^m a second. Muslin exposed for 1^h 15^m, at a distance of 9^m from the water. Salinity of spray sample 0.673 per cent., of sea water 0.662 by areometric measurement, and 0.632 per cent. by chemical analysis. Temperature of water 15°.0 C. As is the case in this observation the areometric value of salinity is always somewhat higher than that obtained by analysis.

II. Hangö Tulludd, Finland, September 9, 1897. Atmospheric temperature 21°.2 C. Sky partly overcast. Velocity of offshore wind about 10^m a second. Muslin exposed on the beach, 5^m from water, for 2^h. Salinity of spray sample 0.625 per cent., of sea water 0.607. Water temperature 13°.6 C.

III. North Beach, near Perth, Western Australia, September 16, 1902. Atmospheric temperature 24°.6 C. Sky clear. Velocity of wind, measured with anemometer (of Crova type, from NEGRETTI & ZAMBRA, London) averaging 12.3^m a second during time of observation. Muslin exposed on the beach, 8^m from the water, for 4^h 15^m. Salinity of spray 4.68 per cent., of sea water 3.24 per cent. Temperature at the surface 10°.6 C.

IV. Beach at Pialba, Queensland, on the eastern coast of Australia, June 17, 1901. Atmospheric temperature 16° C. Sky clear. Velocity of wind about 6^m a second. Muslin exposed 5^m from the water. A heavy surf was rolling at the time, but as the water is shallow far out from shore, and sheltered by clumps of mangrove, the breakers did not strike the shore with any force. The sample showed a salt content of 4.1 per cent. Salinity of ocean water 2.91 per cent., and temperature 9°.4 C.

Although the presence of sodium and chlorine, as common salt, can be shown in many inland plants, a larger percentage of these salts is found in the ash of strand and marine plants than in that of the former type.

Whether these salts are absolutely essential for any plant we do not know for certain. If that is the case, the amount of salt needed is very small, as has been shown by several investigators. Even for many marine algae only the smallest quantities of salt are necessary, if at all essential.

Inland plants are, however, unfavorably influenced by a percentage of salt which strand plants bear without injury; on the other hand, it has been proved by cultures, that the halophytes can grow without the usual amount of salt contained in the soil or atmosphere of their natural habitat.

An interesting experimental study of strand and other plants with relation to common salt and sea water has been made by COUPIN (**5**). He found that 1.5 per cent. of common salt in soil or in water is poisonous to plants which do not naturally grow on the sea shore. Sea water contains about 2.5 per cent. of common salt, and the soil washed by the sea, as well as the atmosphere near the coast, contains still more than this proportion. We can thus readily understand the sharp line which separates the marine and strand floras from those of the interior. COUPIN attributes the poisonous property of sea water for inland plants mainly to its content of common salt, for the two salts next to this in abundance, magnesium sulfate and magnesium chlorid, are present in quantities which he considers below the toxic proportions. Magnesic sulfate is poisonous at a concentration of 1 per cent., magnesic chlorid at 0.85 per cent., but they occur in sea water only to the extent of 0.75 per cent. and 0.5 per cent. respectively.

The question of the influence of salt on strand plants and of the absorption by the plant of saline water has been discussed considerably, and several theories have been advanced.

PRECIPITATION is a factor, which on naturally dry soil, such as presented by sand formations, is of considerable importance, not only on account of the quantity of water which in this way is brought to the plants, but also because of its influence in giving coherence to the sand, thus preventing it from shifting, and because of its weathering action on the soil particles.

That precipitation must to a great extent influence the development of vegetation on marine coasts is evident, and it is easily seen that the composition of the plant covering of sand formations varies somewhat in rainy and rainless climates, although the atmospheric humidity on the coast tends to minimize this difference. The latter factor is especially important as the precipitation often is so variable. The absolute amount of rain during the year does not in fact give any correct basis for comparison of the conditions in different localities, as it is far more important for the vegetation how this quantity is distributed over the period in question. On the Baltic shores the number of rainy days of the vegetative season is much greater than, for instance, on the coast of Australia or California. The eastern coast of Australia, at Brisbane, has an average yearly rainfall of 129.5$^{\mathrm{cm}}$ while the Åland Islands in the Baltic have only 52.9$^{\mathrm{cm}}$, but the vegetation in the latter region has a much more even supply of moisture during the vegetative season, because the precipitation is distributed over a greater number of days, about 70 of the 160 rainy days of the year falling in the growing season.

Edaphic factors

When SCHIMPER proposed this term (1898) he apparently regarded it as covering all the peculiarities of the ground. It seems to the present writer that it would be more convenient in this connection to distinguish between the soil as such, and the media, water and air, filling the interstitial spaces. This distinction has been made in this paper by separating the factor of soil moisture under the heading *hydrodynamic*, and the factors pertaining to the soil proper as *edaphic*.

The hydrodynamic factors are now generally admitted to be of the very greatest importance for the vegetation and its distribution. I have treated this subject in another place (**12**). With regard to the edaphic factors, *sensu scriptoris*, a wide difference of opinion has prevailed. While some writers have maintained that the chemical influence of the soil is the most important, others have been in favor of the theory which gives to the physical properties of the soil the largest bearing. Since the physical conditions mainly determine the amount of water, most recent authors upon the subject, among them WARMING, hold that these are of greater consequence.

In discussing the physical conditions of sand formations we will confine ourselves to the question of soil temperatures, and further briefly refer to some measurements of the size of sand grains made by the writer.

SOIL TEMPERATURE.—The heat-absorbing power of sand is low in comparison with other darker-colored soils, but because the radiation is great the vegetation on a surface of sand is subjected to a comparatively high temperature. As the sand is always moist only a little below the surface the heated layer of sand does not reach deep before it meets lower temperature.

The roots always penetrate to this moist layer, and only the upper part of the root is under the influence of the heat of the surface stratum of sand. We find corresponding adaptational protections on the roots of most plants growing in sandy soils.

The transport of heat within the soil is influenced by several factors outside the conductivity from one layer to another. It is impossible, however, in the natural state of the soil to eliminate these factors, the movements of water and air in the soil, the evaporation of water from the warmer and condensation of water vapor in the colder strata. The data here supplied therefore represent the temperature of the soil under conditions such as it presents in the field.

In all observations made by the author ordinary soil thermometers were used, and the temperature was taken at following depths: 2, 5, 10, 20, and 50^{cm}. The bulb of the instrument can easily be placed in loose sand at the desired depth. The number of complete series of observations made on different sand formations reaches 876. Some of these will here be referred to, and in other cases average values will be given.

On the front beach the temperature of the soil is varying more than on other formations of the sand strand, because of the frequent inundations and subsequent changes in evaporation. It is generally low as compared with that on the higher parts of the beach. Seven measurements taken at Högsar, Nagu, Finnish Archipelago, in June, 1894, averaged 16°.4 at a depth of 2^{cm}. The corresponding data, obtained at varying depths, are shown by Table I.

TABLE I

	2 cm.	5 cm.	10 cm.	Air	Sea water	Time	Wind velocity, m. per sec.	Cloudiness 1–10
1..........	18.3	16.3	17.4	19.6	18.4	12:30 P. M.	1.5	2
2..........	14.9	15.5	16.3	13.8	16.6	2:00 P. M.	0.5	6
3..........	19.6	18.9	18.6	19.8	16.7	11:30 A. M.	4.1	4
4..........	16.5	15.8	15.9	16.5	16.9	2:00 P. M.	0.3	0
5..........	14.2	14.6	15.2	14.4	16.5	1:30 P. M.	2.6	1.5
6..........	13.3	13.6	12.9	14.0	15.6	1:30 P. M.	1.8	2
7..........	16.7	15.4	14.7	16.9	16.5	2:00 P. M.	0.4	1

In all cases except 3 the sand was covered with vegetation, in 5 and 7 with *Glaux maritima*, in 2 with *Erythraea litoralis*, in 1 and 4 with *Argentina anserina*, and in 6 with *Triglochin maritimum* and *Eleocharis uniglumis*.

In September, 1902, similar measurements were taken on the front beach at Freemantle, Western Australia. No vegetation occurred on the formation. The following results were obtained (Table II):

TABLE II

	2 cm.	5 cm.	10 cm.	20 cm.	Air	Sea water	Time	Wind velocity, m. per sec.	Cloudiness 1–10
1....	32.6	25.4	22.9	20.2	26.4	13.4	9:00 A. M.	2	1
2....	37.4	28.7	27.1	24.9	30.1	14.6	1:00 P. M.	2	1.5
3....	26.2	19.2	17.4	15.6	27.5	12.9	2:00 P. M.	1.5	3
4....	25.4	20.4	18.5	15.8	24.4	12.5	11:30 A. M.	0.3	6
5....	21.3	15.6	14.2	13.6	22.7	12.8	12.15 P. M.	3.5	4

The average temperature of these five series at 2^{cm} depth is thus 28°.5 C., that is, 12°.1 higher than the mean of the previous series. The sea water in the latter case was much colder, while the atmospheric temperature was considerably higher.

Of sixty measurements taken in day time on the front beach under conditions as similar as possible, the highest temperature obtained for 2^{cm} depth was 42°.6 C. on the Queensland coast at Pialba, in December, 1901, while the lowest was 2°.1 near Mariehamn, Finland, in September, 1896. The average of these sixty observations was 18°.4 C.

The soil temperature on the middle beach is already much higher, as following data will show. The observations were made at the same time and in the same place as those mentioned in Table I. The distance from the water was 6.5^{m} and the sand pure quartz of medium size and yellow color.

TABLE III

	2 cm.	5 cm.	10 cm.	20 cm.	50 cm.
1	22.6	20.1	17.8	14.1	12.6
2	19.1	16.7	14.9	12.7	12.1
3	23.4	21.3	18.9	15.3	13.3
4	20.1	18.5	17.0	13.9	12.7
5	18.4	16.9	15.6	12.7	12.2
6	16.9	15.2	13.7	12.6	11.9
7	19.8	17.3	15.5	13.8	12.9

The vegetation consisted in 1 and 3 of an open community of the following constituents:

FACIES: *Leontodon autumnale*, copious.

SECONDARY: *Festuca rubra arenaria*, subcopious, *Agrostis vulgaris*, subcopious, *Plantago maritima*, gregarious, *Erythraea litoralis*, sparse.

In 2 Erythraea was scattered about in patches, between low shrubby *Alnus glutinosa*, solitary individuals of *Elymus arenarius*, and *Rosa canina*.

In 4, 5, and 7 a *Juncus Gerardi* community occurred on the middle beach, with sparse *Erythraea litoralis* and *Plantago maritima*. In 6 *Elymus arenarius* and *Festuca rubra arenaria* formed an open community.

A parallel table to Table II shows the temperature conditions on the middle beach at Fremantle, W. Australia. The sand was here fine, consisting of pure light-yellow quartz. Time and atmospheric conditions as in II.

TABLE IV

	2 cm.	5 cm.	10 cm.	20 cm.	50 cm.
1	35.2	23.4	22.4	20.7	18.4
2	38.6	25.8	24.6	23.6	20.0
3	29.5	18.6	18.3	16.5	15.8
4	27.2	21.3	19.6	17.2	16.3
5	24.6	16.9	16.1	14.9	14.4

A comparison with the results in Tables I, II, and III reveals the fact that, while the surface temperature (2^{cm}) in all cases was higher in the series given in Table IV than in Table II, the temperatures at 5^{cm} and lower were higher in the former case, presumably on account of a more intense evaporation, which caused a corresponding loss of heat. No such difference existed between Tables I and III, where the solar radiation was less, and both the atmospheric and sea-water temperature lower.

We shall now proceed to a statement of the temperature conditions on the upper beach. Table V gives the results of some observations made on that formation at Jerwe on the Oesel Island in the Baltic, in July, 1896. The beach has a low grade and is limited landward by a littoral dune in the shape of a steep and high bank, on the top of which small dunes are developed. The sand on the upper beach at the foot of this bank is rather coarse, consisting of a reddish-yellow quartz.

TABLE V

	2 cm.	5 cm.	10 cm.	20 cm.	Air	Sea water	Time	Wind velocity, m. per sec.	Cloudiness
1 . . .	22.4	22.8	21.4	19.6	21.6	17.1	10:30 A. M.	1	3
2 . . .	27.3	26.2	24.5	22.7	25.2	16.4	1:00 P. M.	0.5	1
3 . . .	26.8	24.3	22.8	21.1	23.6	16.1	3:15 P. M.	2	5

The next table is a continuation of the measurements given in Tables II and IV from Fremantle, W. Australia, and the general conditions supplied in regard to those tables refer also to these observations on the upper beach, except that the time in each case was about 15 minutes later. The sand was of medium-sized, white-yellow quartz, mixed with an abundance of shell fragments.

TABLE VI

	2 cm.	5 cm.	10 cm.	20 cm.	50 cm.
1.	34.8	24.5	22.6	21.1	18.3
2.	38.9	24.9	23.4	22.0	19.6
3.	28.8	19.2	17.6	16.4	14.8
4.	27.6	22.5	20.7	18.2	16.6
5.	25.3	17.3	16.9	14.5	13.8

As will be seen, the temperature on this formation does not differ essentially from that on the middle beach at the same locality as given in Table IV. The differences existing may be accounted for by the topography and by the fact that the upper beach here was covered with a sparse vegetation consisting of various low herbs.

On the littoral dune the temperature conditions are somewhat varying, usually higher on the landward slope, and a rise in temperature can also be noticed with an increase in the height of the dune. The summit and the landward slope of the littoral dune are frequently covered in large patches with vegetation, and the temperature differences between the open spots and those where plants occur are considerable.

Table VII shows a series of measurements made on the seaward slope of the littoral dune at Fremantle, W. A., under conditions similar to those given for previous observations from that locality. The sand was fine white quartz.

TABLE VII

	2 cm.	5 cm.	10 cm.	20 cm.	50 cm.
1............	35.2	26.4	23.5	21.5	19.2
2............	38.8	27.3	22.6	20.6	18.4
3............	29.4	20.5	18.1	16.2	15.4
4............	28.9	21.3	19.4	17.7	16.2
5............	25.6	18.7	16.6	15.1	14.3

Table VIII gives the temperature on the summit of the same dune, at a height of 6^m over the ocean level. The dune material consisted of medium sand, somewhat yellowish in color.

TABLE VIII

	2 cm.	5 cm.	10 cm.	20 cm.	50 cm.
1............	35.5	27.4	24.2	21.7	19.8
2............	38.8	28.1	23.0	21.2	18.9
3............	30.3	21.0	18.2	16.8	15.7
4............	30.1	21.8	18.9	18.3	16.3
5............	26.4	18.8	16.7	15.7	14.0

On the landward slope, some 3^m from the top, the following measurements were obtained:

TABLE IX

	2 cm.	5 cm.	10 cm.	20 cm.	50 cm.
1.	35.4	27.0	23.6	21.5	19.4
2.	39.2	27.6	22.8	20.4	18.2
3.	29.8	20.8	18.1	16.5	15.6
4.	29.5	21.7	19.0	17.8	16.1
5.	25.9	18.9	16.8	15.6	14.3

In this last case the sand was rather fine quartz, of yellowish color. The maximum soil temperature measured by the author on a littoral dune formation was obtained in December, 1901, on the leeward slope of a high dune at Southport, Queensland, where the thermometer 2^{cm} under the surface registered 58°4 C. at 2 P. M. The formation was devoid of vegetation.

The temperature of the dunes and the sand fields varies greatly. Some averages will be here given. Of the 34 readings made under general conditions as similar as possible a mean temperature of 26°2 C. was obtained from dunes in Finland for a depth of 2^{cm} and 25°4 for 5^{cm}. The average of 19 readings at Fremantle, W. A., was 28°7 C. and of 12 readings at Southport, Queensland, 29°8. On the dunes of North Cape, New Zealand, the author measured on the same day within one hour the following series: 26.1, 25.8, 24.2, 27.9, 25.4, 26.3, 26.1, 27°9 C. The atmospheric temperature at the time was 25°4, cloudiness 3, time December 7, 1902, 11:30 A. M.–12:30 P. M.

The daily variation of temperature must naturally be of some importance to the vegetation. Only a few observations have been made by the writer to this end. One series will be given as a sample of the extent to which such variations take place. The readings were made at Southport, Queensland, in December, 1901.

In the light of measurements obtained the local distribution of certain plants on the coastal sand formations seems to indicate that the temperature factor is of the greatest importance for the mode of association of plants into communities. On the coasts of the Baltic the writer made frequent observations which tend to show this.

At Åhus in Sweden there occurs on the upper beach an Ammophila-Elymus community, consisting of the following plants:

FACIES: *Ammophila arenaria, Elymus arenarius.*

SECONDARY: *Triticum junceum, Carex arenaria, Festuca rubra arenaria, F. ovina, Poa pratensis, Cakile maritima, Halianthus peploides.*

TABLE X

HOUR OF READING	ATMOSPHERIC TEMPERATURE	DEPTH UNDER SURFACE					CLOUDINESS 1–10
		2 cm.	5 cm.	10 cm.	20 cm.	50 cm.	
6 A. M.	9°6 C.	4.9	4.2	5.7	9.1	14.3	6
7	10.8	6.5	5.6	5.9	9.4	14.4	2
8	11.4	7.7	6.9	6.2	9.4	14.6	3
9	15.6	9.0	8.9	6.9	9.6	14.6	1.5
10	17.7	11.2	10.2	8.0	9.7	14.5	4
11	19.5	14.6	11.8	9.6	9.8	14.5	3
12 NOON	23.2	17.2	13.0	10.5	10.1	14.7	3
1 P. M.	26.3	19.6	14.3	11.8	10.7	14.4	5
2	27.2	19.4	14.8	12.6	11.4	14.5	4
3	27.0	18.1	14.6	12.7	11.6	14.5	4
4	26.4	18.0	14.3	12.6	11.8	14.4	5
5	25.1	17.3	14.0	11.8	11.6	14.5	4
6	22.3	15.1	13.5	11.2	11.7	14.6	2.5
7	18.6	12.9	12.3	10.4	11.9	14.6	1
8	16.2	11.0	10.7	9.5	11.6	14.7	0.5

The two species which constitute the facies of this community usually occur in small separated patches, and measurements of the temperature in the small sand elevations formed by these plants revealed the fact that in the Ammophila patches the soil temperature almost invariably was two-tenths to six-tenths of a degree higher that in the latter case, which would explain the lower temperature, but the exact difference in moisture has not been ascertained. Many similar instances of temperature differences have been noticed. *Halianthus peploides* always grows in colder places than *Argentina anserina*, although both together often form a community. This question of temperature differences influencing the formation of communities, however, needs further investigation before any decisive statements can be made. It must also be remembered that the temperature is influenced by the moisture, which in its turn depends to a great extent on the physical conditions of the soil.

MECHANICAL ANALYSIS OF SAND.—A considerable number of such analyses have been made by the writer, and a few series will here be given to show approximately the differences in size of sand grains on the various formations on different sand strands. In the table the letter *A* refers to a series of samples from Kurische Nehrung on the northern coast of Germany, *D* to a series from sand formations near Amsterdam in Holland, *E* to sand from the west coast of France south of Bordeaux, *F* to samples from the west coast of Australia, near Fremantle, *G* to sand from Port Fairy, Victoria, *H* to the sand at Southport, Queensland, *I* to a series from North Cape of New Zealand, and *J* to a series of samples from the Pacific coast of North America near San Francisco.

	A	B	C	D	E
Submerged beach	Finest	Medium	Medium	Fine	Finest
Front beach	Fine	Medium	Fine	Fine	Coarse
Middle beach	Fine	Fine	Coarse	Medium	Coarse
Upper beach	Coarse	Medium	Coarse	Medium	Grits
Littoral dune	Medium	Fine	Medium	Fine	Medium
Dunes	Medium		Medium	Fine	Medium
Sand field		Finest			Finest

	F	G	H	I	J
Submerged beach	Coarse	Medium	Fine	Coarse	Medium
Front beach	Medium	Fine	Medium	Grits	Fine
Middle beach	Medium	Medium	Coarse	Coarse	Fine
Upper beach	Coarse	Medium	Coarse	Grits	Medium
Littoral dune	Medium	Fine	Medium	Medium	Fine
Dunes	Fine	Fine	Medium	Fine	Fine
Sand field		Finest			

In each of the above cases the result represents the average of 10 samples, secured at approximately corresponding places on each formation. As these data show, the coarsest sand occurs on the upper beach. The material that builds up the littoral as well as the ordinary dunes is usually of the same grade of coarseness. It is only when we analyze the sand from various places on the dunes that differences appear, which explain the formation of ripple marks and dunes as discussed on previous pages. It will be seen when we describe the vegetation on the various formations that the coarseness of the sand in some cases seems to determine the composition of the plant communities. This is easily understood when we consider that the size of the sand particles determines the water-holding capacity of the soil.

CHEMICAL COMPOSITION OF SAND.—The nutritive value of sand is different according to the chemical character of the sand grains. As a rule, sand is very deficient in plant food, and this is especially the case with the commonest form of sand, that which consists mainly of quartz. The quartz grains are insoluble, or only to a very small degree soluble. Only in the case of lime or organic matter in the form of humus entering into the composition of the sand is there plant food in sufficient quantities to allow the development of a more luxuriant vegetation. Generally the chemical composition of coastal sands is very uniform, and this may to some extent account for the evident similarity in vegetation on these formations.

A number of analyses of sand have been made by the writer, and some typical results will be here related.

No. 1.—Middle beach, Eckerö Storby, Åland Islands, Baltic

	Per cent.		Per cent.
Insoluble matter	89·25	Alumina	1·38
Soluble silica	3·44	Water and organic matter	2·57
Lime	1.06	Nitrogen	0.16
Potash	0.18	Other constitutents	1.02
Phosphoric acid (soluble)	0.24	Total	100.01
Peroxid of iron	0·71		

No. 2.—Littoral dune, Engelholmshamn, Skåne, S. W. Sweden

	Per cent.		Per cent.
Insoluble matter	84·38	Alumina	1·83
Soluble silica	4·53	Water and organic matter	4·93
Lime	1.04	Nitrogen	0.12
Potash	0.21	Other constitutents	2.00
Phosphoric acid (soluble)	0·33	Total	99·99
Peroxid of iron	0.62		

No. 3.—Upper beach, North beach, near Perth, W. Austr.

	Per cent.		Per cent.
Insoluble matter	86.32	Alumina	0.93
Soluble silica	3·61	Water and organic matter	2.89
Lime	1·53	Nitrogen	0.03
Potash	0·36	Other constitutents	3·33
Phosphoric acid (soluble)	0.15	Total	100.02
Peroxid of iron	0.87		

No. 4.—Dunes, Southport, Queensland

	Per cent.		Per cent.
Insoluble matter	91·90	Alumina	1.08
Soluble silica	3·18	Water and organic matter	2·15
Lime	0.86	Nitrogen	0.11
Potash	0.21	Other constitutents	0·44
Phosphoric acid (soluble)	0.29	Total	100.00
Peroxid of iron	0.08		

No. 5.—DUNES, GOLDEN GATE PARK, SAN FRANCISCO, CAL.

	Per cent.		Per cent.
Insoluble matter	88.27	Alumina	1.08
Soluble silica	4.42	Water and organic matter	2.15
Lime	1.94	Nitrogen	0.05
Potash	0.17	Other constitutents	1.80
Phosphoric acid (soluble)	0.08	Total	100.01
Peroxid of iron	0.05		

These analyses show what a small amount of plant food is available in the dunes in comparison with that in ordinary agricultural soil, where the insoluble substances do not comprise more than 70 per cent. of the total volume. And it must be remarked that the analyses here given represent soil from places more or less covered with vegetation, where the organic constituents are better preserved from decomposition and from being washed out by water than on open sand. They therefore show a higher percentage of humus and soluble material than the barren quartz unprotected from the influence of sun, air, and water. Where sand has recently been deposited after having been exposed for some time to sea water it is naturally very deficient in plant food, and it has therefore to be considerably changed before it is able to sustain a vegetation covering.

The amount of lime contained in the dunes varies to a great extent. On tropical coasts it is generally very large, especially where the sand is formed by disintegration of coral rocks. On such shores carbonate of lime is dissolved by the rain water and the sand is at a low depth under the surface consolidated into limestone. A similar process of calcification can be observed also on many coasts where the amount of lime is quite small, as on some coasts of Europe. BANG (1) has observed that the dune sand near the sea contains up to sixteen times more lime than farther inland. This is a natural result of the washing-out process and decomposition, which takes place on the open sand, and is more effective farther inland, because the supply diminishes with the distance from shore.

On the upper beach and on the seaward slope of the littoral dune are frequently found fragments of shells that have been carried ashore by the waves. In places where the littoral dune is broken, shells are often accumulated in the depressions, while more landward the lime in the animal remains is disintegrated by the carbon dioxid of the rain water.

The greater or smaller amount of peroxid of iron in dune sand determines to some extent its color. The usually colorless grains of pure quartz are covered with a thin coat of ferric hydroxid, which gives the sand its yellow color, and in some places almost a red tint.

THE SOLUBLE SALT CONTENT IN COASTAL SAND.—Of the soluble salts that saturate the coastal sands sodium chlorid is the most important. Its presence, as common salt, in all plants is well known, and its influence on the littoral flora is very apparent. Whether sodium chlorid is essential to plant life is still an open question, and the investigations hitherto conducted in order to ascertain this fact seem to indicate that such is not the case. In experiments it is difficult to eliminate salt entirely, but it has been conclusively shown that the smallest quantities only, if any at all, are needed for the development of plants, even for those which apparently prefer salty situations, when growing under natural conditions.

That common salt is injurious to plants, when present in excessive quantities, is certain. It is commonly believed that this unfavorable influence of salt is due to the amount of magnesium chlorid it contains. It is more likely, however, that all the chlorids are injurious, and experiments by the writer have supported this view, previously maintained by several authors.

It is generally stated by various writers that the formations on the sea coast contain a considerable amount of common salt. Thus WARMING (**14**) says that on the sandy beach the salty ground water is found at only a slight depth under the surface. CONTEJEAN (**3**), in speaking of the conditions in southwestern France, considers that his second belt of sea-shore vegetation, that is our middle and upper beach, is growing in a saline soil. MASCLEF (**9**) found the salt content in dunes near the sea to be 0.351 per cent., while at a distance 150^m from the shore he found 0.17 per cent. of sodium chlorid, and at 1500^m he discovered 0.041 per cent.

There has been some doubt, however, in the minds of certain authors whether the coastal dunes are impregnated with common salt or not. Among these is MASSART (**10**). The present writer has on various coasts made tests for salts in the sand by means of chemical analysis. The result of these observations shows that under ordinary circumstances *dunes do not contain sodium chlorids in perceptible* *quantities.* When salt is found *it has been deposited as spray from the sea*, but this is rapidly washed out by rain water, and when no precipitation has fallen, the *sodium chlorid does not come into contact with the ground water but is detained on the surface by the upward movement of the water.* Because of this the roots of the plants are not exposed to sodium chlorid. On the littoral dune the uppermost half an inch layer of sand usually contains some salt, but deeper in the soil no salt is found before we reach the sea-level. The upper beach has very similar conditions, as a rule, except at times when inundated by high water. Even on the middle beach we cannot find that the sand would be impregnated with salt. On the contrary, for quite a considerable depth there is fresh water, which, on account of its being lighter than the salt water, flows on top of the latter. This fresh water is a part of the continuous stream of rain water, which slowly works its way to the sea. The roots of the plants do not, as a rule, penetrate deeper than to the bottom of this fresh-water layer, and it is therefore wrong to assume that the plants are growing in salt water on the beach. Even on the front beach, the layer in which the roots of the plants are situated has more of a brackish character, because the water from the beating waves runs off before it has time to sink through the layer of fresh water, which flows on the surface of the salty ground water.

On a superficial investigation of the beach it appears that the ground is thoroughly soaked with salt water, but careful sampling from various depths and subsequent analysis has made it apparent to the writer that this is not the case. It is a well-known fact, however, that the ash of strand and marine plants contains a much larger percentage of sodium chlorid than that of inland plants. This is due, of course, to the presence of a greater amount of salt on the sea shore than inland. But when it comes to a comparison between the conditions on sea shores and salt-impregnated formations in the interior, the amount of salt in the latter is much greater. This fact brings forward the question whether all sea-shore plants are halophiles or not. KEARNEY (**8**) has investigated this question and comes to the result that they are not. The present writer made numerous experiments in this direction and the results confirm those of KEARNEY, as the following discussion will show.

It has long ago been proved by experiments that most inland plants are injured by the presence in the soil of sodium chlorid in certain quantities, which the strand plants are able to tolerate without evident injury. There appears to be a certain maximum amount of salt for every species, to which it is very accurately adapted, and this maximum cannot be overstepped without fatal results to the plant. In some cases investigated by the writer this maximum has been found to be:

	Per cent.		Per cent.
Argentina anserina	1.9	*Glaux maritima*	2.7
Aster Tripolium	2.6	*Juncus Gerardi*	2.2
Atripex hastata maritima	3.1	*Matricaria inodora maritima*	2.3
Cakile maritima	2.9	*Plantago maritima*	2.8
Crambe maritima	2.5	*Sonchus arvensis maritima*	2.6
Elymus arenarius	2.6	*Triglochin maritimum*	2.1
Erythraea vulgaris	1.9		

These experiments were conducted in the summer of 1894 with plants from the Baltic coasts. Sand cultures saturated with normal solution of sodium chlorid were used. In these cultures young seedlings as well as older plants were grown, and the results given above refer to seedlings, about two weeks old at the time of transplanting. They were grown in fresh water for five days, after which time the salt solutions were gradually applied. It was found that plants which had been growing on strands with low salinity were considerably more sensitive to an increase in the amount of salt than those which were brought in from the open shores with higher salt content in the water. Strong, well-developed plants adapted themselves more readily than weaker specimens to the gradual transfer to stronger salinity. It would be of considerable interest to ascertain whether this specific limit of salt concentration could be raised much higher by growing the plants through a succession of seasons. The ability of the seashore plants to endure salt in the soil without injury and by adapting themselves to these conditions has, no doubt, been the ultimate cause of their being in many cases confined to the strand, precluding competition from forms not possessing this power of resistance.

We also know from experimental cultures that strand plants do not need sodium chlorid in order to develop normally. The question then arises whether the common salt, even when present in quantities lower than the maximum, exercises a poisonous influence or not. Schimper, who paid much attention to this matter, came to the conclusion that the chlorids produce abnormal conditions in the plants and disorders in the nutritive processes. In this regard most writers agree, but in explaining the means by which the plant neutralizes this injurious effect of common salt there is a wide divergence of opinion. While SCHIMPER maintains that the structural adaptations of halophile plants are caused by the necessity of keeping the relative amount of sodium chlorid in the cell-sap below the specific danger point, DIELS (**6**) considers that this is effected by chemical decomposition of the salt. This process is not known, but DIELS assumes that in respiration the succulent halophytes differ from other plants in that the oxidation does not proceed so far in halophytes, but stops at malic acid or some isomer, with which the cell-sap becomes saturated, while only small quantities of carbonic acid are evolved. The malic acid then combines with the hydrochloric acid and is excreted by the roots. BENECKE (**2**) has severely criticized these conclusions of DIELS.

In regions having a hot climate the evaporation of water is very great on the coastal sands and the salinity is naturally higher. The concentration of salts is also increased in countries where the rain falls only during a rainy period, leaving a long time in which no leaching of the salts takes place in the soil. In places with frequent rains the salts are rapidly washed out and carried deeper into the ground, until the lateral flow of water toward the sea is encountered.

The observations on salinity of strand sand made by the author are all based on chemical analysis. The electrical method of determining the salinity as employed by the United States Bureau of Soils was not familiar to the author at that time, but careful observations and determinations of the salinity with that method ought to reveal the causes of distribution of certain plants on the strand. The writer has found that *the small embryonic dunes formed by certain strand plants contain a greater amount of salts than those occupied by others.* Thus, for instance, the small, embryonic, *Elymus arenarius* dunes always contain 0.005–0.009 per cent. more sodium chlorid than the *Ammophila arenaria* dunes. Likewise the Mesembryanthemum dunes on the California coast have a higher salinity than the Abronia dunes, while the elevations formed by *Abronia latifolia* contain more salt than *A. umbellata* hummocks. These are the only examples which have been verified by analyses, but more extended investigations will, no doubt, give an explanation of certain hitherto unexplained features of the local distribution of strand plants.

We often find on sandy sea shores a number of immigrants from inland formations, and this occasional occurrence of plants which do not naturally belong to such habitat shows that it cannot be the chemical composition of the salt water that keeps so many island plants from the sea shore, but other adverse conditions, which allow only the peculiar sand-strand flora to develop. Even on the front beach, where the salinity is greatest, we cannot attribute the scarceness of the plants to the salt content, but to the easily movable sand soil.

As we have already mentioned, the lateral current of fresh water flowing on the surface of the salty ground water near the sea has to be taken into consideration when we discuss the salinity of the strand soil. Our assumption that the conditions of the strand are not such as to characterize this formation as halophytic is borne out by the analyses made of the salinity of the soil at different depths. Many true halophytes, of course, occur on the sea shore, but the strand flora as such must rather be classified as a halophile flora, while the true halophytes are those plants which are confined to saline situations in the interior, or where we know that the hydrodynamic conditions do not change to any marked degree the salinity, as is the case on the sea shore. If this holds good, the halophytes occurring on the strand must be regarded as immigrants from dry saline habitats.

Several Salsolaceous plants, widely spread in the interior of Australia, sometimes occur on the sea shores of that continent as straggling poor specimens, but reach their best development in the dry saline soil of the interior. SCHIMPER (13) maintains that the cliffs on the sea shore have a much less halophile flora than the sandy or marshy strands. This is evident to everyone who has studied the strand floras, but we shall find that the plants even on the cliffs exhibit many characters of the halophytes, and are sufficiently differentiated from the cliff vegetation of inland situations to warrant a classification as halophile. The physical nature of the substratum prevents its being impregnated with common salt. We have here to account for the development of adaptations so characteristic for halophytes, not so much through the influence of salt in the soil as through the salt contained in the spray, to which the plants are constantly exposed. On sandy soils the protectional adaptations are caused more through the physical conditions of the sand, than through the salt content of the soil. The characteristic vegetation developed on all sand formations, inland as well as on the coast, is so much alike, that there is no reason to assume that the sodium chlorid content of the sea shore, which in fact is not very large, would be responsible for the aspect of the vegetation on marine sand strands. On coastal marshes the conditions are different, and this is also evident in the vegetation on such formations, which in no way differs from that on saline marshes in the interior, and always is composed of true halophytes.

A series of samples of the soil was taken with earth-auger on the beach and dunes at Fremantle, Western Australia, at various depths, and subsequently examined for soluble salts. The results appear in Table XI.

TABLE XI

Date	Formation	Distance from high-tide mark in meters	Character of soil	Depth in cm.	Angle of slope	Temperature ° C.	Degree of moisture 1–10	Percentage of salt	Notes
Dec. 18, '02	Lower beach, upper limit	2	Medium sand	20	15	18	9	0.005	
	Middle beach	5	Medium sand	35	21	20	6	0.004	Sparse vegetation
	Border of middle and upper beach	7	Coarse sand	30	23	20	6	0.004	
	Upper beach	10	Medium sand	30	26	22	4	0.009	
	Dune inside littoral dune	28	Fine sand	40	10	23	5	0.003	
	Littoral dune	15	Fine sand	40	30	21	4	0.007	
	Dune marsh inside littoral dune	29	Finest sand	20	0	19	10	0.005	
Dec. 21, '02	Middle beach	8	Medium sand	25	8	14	4	0.006	
	Same place	8	Medium sand	50	8	12	3	0.004	
	Upper beach	14	Medium sand	25	15	16	3	0.011	Sparse vegetation
				50		15	5	0.006	

Development of humus.—There is no other soil which so little favors development of humus as the loose shifting sand. The organic substances that happen to be deposited on the sand are very rapidly decomposed by the admission of air, and the physical structure of the sand allows rain water to percolate and thus to carry the fine humus particles deep into the soil and out of reach of the roots. The earthworms, which are the most active agents in mold formation in forests, as Darwin and Mueller have shown, are entirely absent in sand and the mycorhizal fungi seem not to thrive on the beach, where they are likely to be exposed to occasional contact with sodium chlorid.

When a shrubby vegetation has got a foothold on the sand, the humus is developed to the best advantage. In the shade of the bushes remains of plants do not decompose so easily as on the open ground, they are more sheltered from the rain, and an accumulation of humus can take place, so that grasses and herbs are able to get a footing. When this has happened the sand is usually made permanently stable. The few animal remains that are thrown up on the front or middle beach enrich the soil on these formations only temporarily, and do not play any important rôle in the formation of the humus on the sand.

Topographic factors

The topography as a factor influencing the development of vegetation is very often overlooked by writers on plant geography. Its importance, however, is so considerable that it cannot be omitted in a discussion of the agents which exert their influence on plant life. On the vegetation topography acts principally indirectly, by determining to a great extent the moisture content of the soil, by influencing the temperature, the exposure to winds, and also the light relations. We intend here to mention briefly only the principal features of topography as far as they influence the conditions on coastal sand formations.

Surroundings.—From our previous discussion (11) of the development of the various sand formations it is apparent that the surroundings are of the greatest consequence to the evolution of dunes. On many of the coasts investigated the topographical conditions have been of such character as to prevent any greater development of dunes. Such was the case, for instance, on the southern shore of the

Gulf of Finland, where almost the whole shore line consists of a steep wall of rock, leaving only a narrow strip of beach along the water edge. In places where this rocky barrier was broken and the winds are allowed free play over a wider stretch of land, dunes appeared at once. The vegetation on the beach of the former type presents a somewhat different aspect from that on open shores with the background of a dune-complex. The best evidence of the influence of surroundings on the composition of the vegetation can be seen if we compare that on a sand field and on a dune-complex with its diversified topography. Also on the slopes of an unbroken dune, the vegetation is usually quite different from that on a train of dunes frequently cut through by furrows and valleys.

On beaches a similar difference can be noticed, and the cause underlying this effect can only be attributed to the topography. Where we have a long continuous beach the plants associate according to rules different from those which have determined the composition of the communities on cuspate forelands. This was especially evident on the shore stretches of sandy beaches that are so common on the shores of the islands in the Baltic.

Elevation.—This factor is of minor importance in regard to the sand-strand vegetation. The sand formations do not rise to any great height, but it seems that certain plants choose their place of growth with reference to altitude, even on these formations. Without taking into account the fact that humus naturally accumulates more rapidly in the depressions, we find that some plants prefer the foot of a dune, while others are found only on the middle of the front slope, and others again do not thrive except on the top of the dune, where they are constantly being covered with drifting sand.

On the beach a corresponding selection of habitat takes place. Some plants never occur on a low beach although the conditions otherwise seem to be favorable, but only a short distance away, where the beach rises more abruptly, they appear again. We have presumably two different causes for this. While on the dunes the selection of a place of growth is determined apparently by the plant's greater or less power of resistance against the drifting sand, on the beach the dominant cause must be the sensitiveness of the plant to inundations of salt water.

Depressions between the dunes offer to many plants a refuge from the sand-laden winds, and the richer soil in the troughs induces other plants to settle.

GRADE OF SLOPE.—We have elsewhere (**11**) referred to this factor as being of great moment in the growth of dunes and in the development of sand formations generally. Its influence on the moisture conditions is of no less importance. The higher up on the slope the drier is the soil, the greater the evaporation, and the more intense the influence of the wind.

The exposure of the slope is another matter of the greatest consequence to the vegetation on the sand formations. The various degrees of slope ought always to be considered when a description of a habitat is given in order to arrive at a correct understanding of the conditions that have determined the composition of the plant community. Southern slopes in the northern hemisphere and northerly slopes in the southern are drier than those facing other directions, and the vegetation has a corresponding aspect. On sea coasts the exposure to the prevailing winds has to be noticed.

Light relations are further to a certain degree determined by the direction of the slope, and this is of special importance in northern latitudes, where light even during the period of growth is not too abundant.

Historical factors

Under this heading we include all those factors whose influence on plant life is determined by time. This must not be understood as if time was not involved in the action of other factors, but that the period of influence and the time required for attaining any results is of such a long duration, that it cannot be ascertained within a few generations of plants. Physiographical changes of land and sea, whether within a century or within long geological periods, have to be considered in this connection. One of the most important historical factors to be looked upon in explaining the present conditions on sand strands is the oscillation of the coast line. The erosion of the shore by waves and the deposition of sand or other material are equally important. Sand deposits are in many places formed so rapidly that the effect can be noticed within a very short time. The influence of animals, principally through grazing, and the intervention of man belong strictly to the group of biotic factors, but have here been considered in connection with the historical factors as a matter of convenience.

Oscillation of the coast line.—Many coasts are slowly rising, while in other instances the coasts are sinking. We have excellent examples of both kinds of movements on the Baltic. While the whole coast of Sweden north of Stockholm, and the coasts of Finland are in a state of elevation, the southern shore of the Baltic is in a corresponding state of depression. Besides having a great influence on the development of dunes, this oscillation of the coast line has had a marked bearing on the evolution of the flora on the coastal sands.

On the shores mentioned which are rising, one may see in some instances how long stretches of land are slowly raised above water and in a few years carry a cover of vegetation that gives an instructive demonstration of the successive stages of development of the plant associations. Again, on the sinking shores of the southern Baltic may be frequently found examples of plant communities being destroyed in the course of a few years through the submersion of the shore.

On the coasts bordering upon the oceans oscillations also take place, but they are usually neither so regular nor so rapid as these changes on the Baltic.

In postglacial times considerable changes of the coast line of the Scandinavian countries have taken place, and as we are able to follow these changes with the assistance of fossil remains of plants, found in old sea beaches now raised high above the present level of the sea, we can to some extent interpret the various stages of development which have been passed before the flora arrived at its present state. This question will be discussed in another paper.

Eolian deposits.—The influence of the wind on formation of plant communities on the coastal sands is shown not only in the peculiar arrangement of the plants in patches, but also in the aspect of the aggregations of plants, which (especially in the case of trees and shrubs) give evidence of being continuously attacked by the strong winds laden with spray or sand. Shrub associations on open strands are usually lower toward the shore, gradually increasing in height inland under the shelter of the more exposed specimens.

Most of the sand-strand plants are not able to withstand partial burying by the shifting sand; consequently it very often happens that whole communities are suddenly destroyed and their place taken up by plants able to endure more or less complete covering by sand. Sometimes it may be observed that trees, which are being buried by

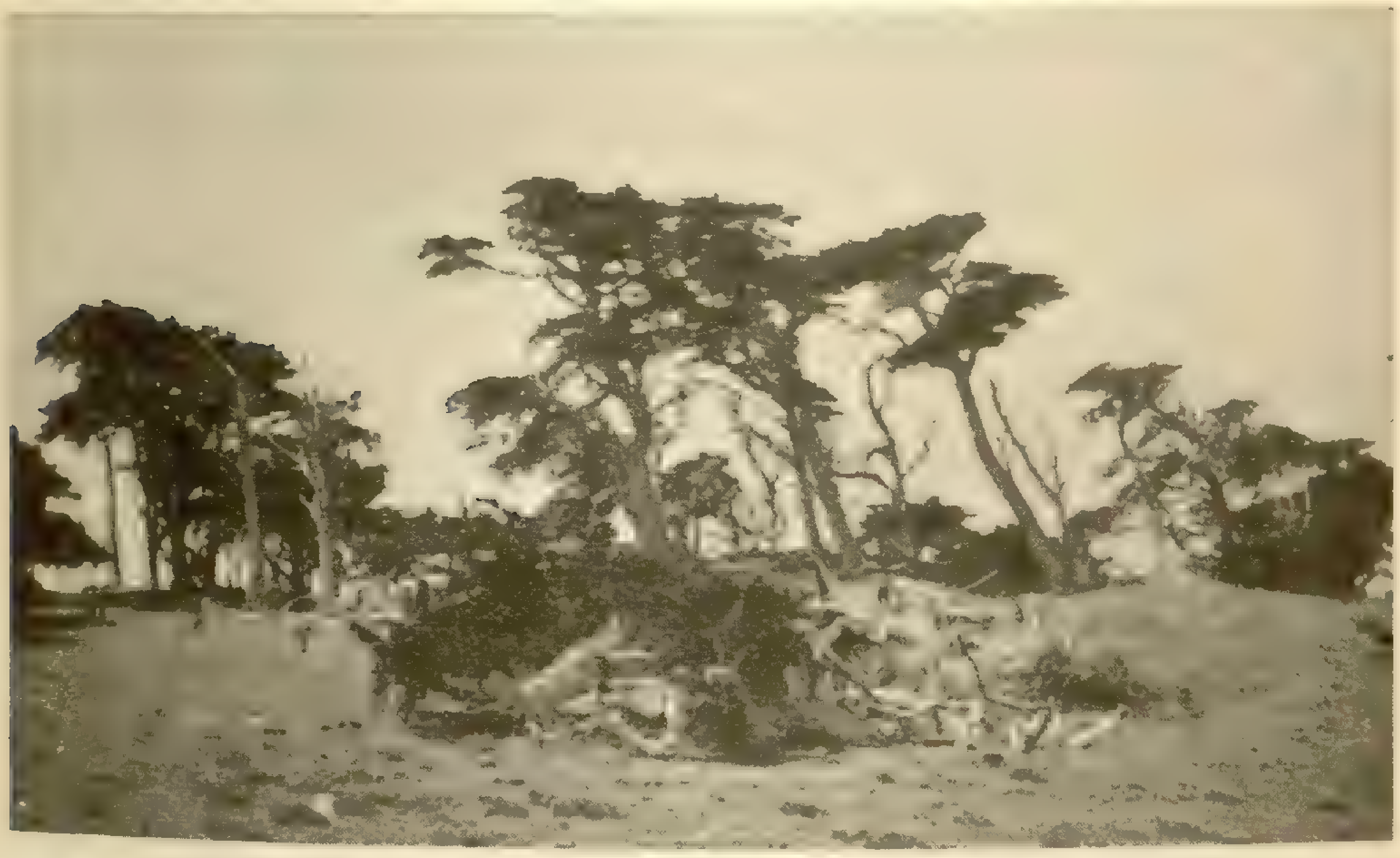

FIG. 1.—*Cupressus macrocarpa* on Cypress Point, Monterey, Cal., showing influence of wind. (Photograph by author.)

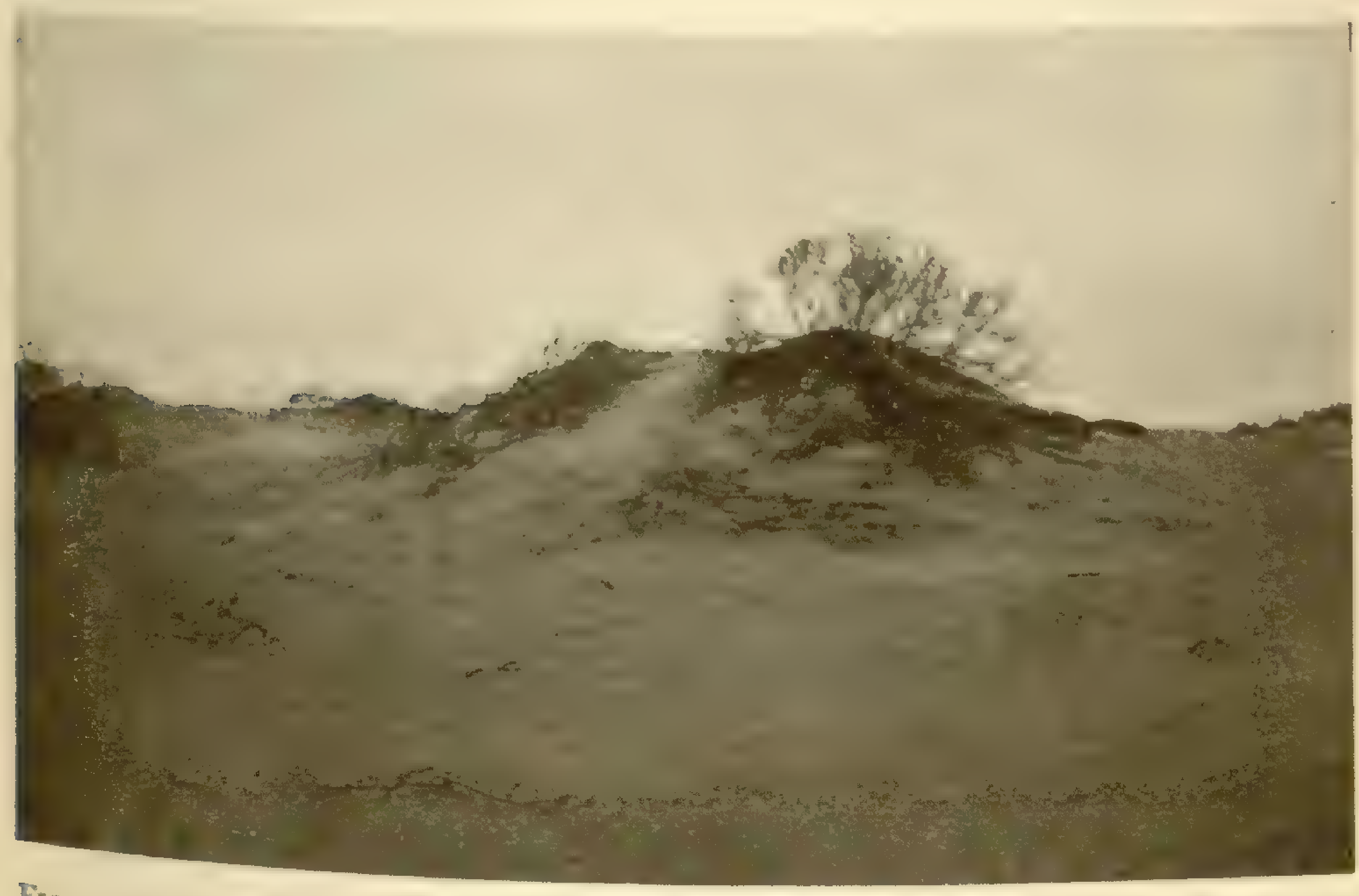

FIG. 2.—Rejuvenated Salix dune at San Francisco, Cal. (Photograph by author.)

an encroaching dune, are bent leeward (*fig. 1*). The cause of this is to be found in the continuous pressure, or in sudden gusts of wind which bend the trees while the onrushing sand prevents return to the original position. As a rule the sand on the lee side of a dune is moister, and the slope is consequently steeper. Often slides of sand take place, and they also bend or even break the trunks of the trees.

Dunes which have been made stable by a cover of plants are sometimes again broken up by the wind (*fig. 2*). Such formations are often met with on the Baltic coasts. On these broken-up dunes the usual series of development of vegetation begins anew and thus they have a peculiar character, remnants of the old communities being mixed with the new immigrants. A new life-history of the plant community is started, and during the course of development it may take a direction entirely different from the former series.

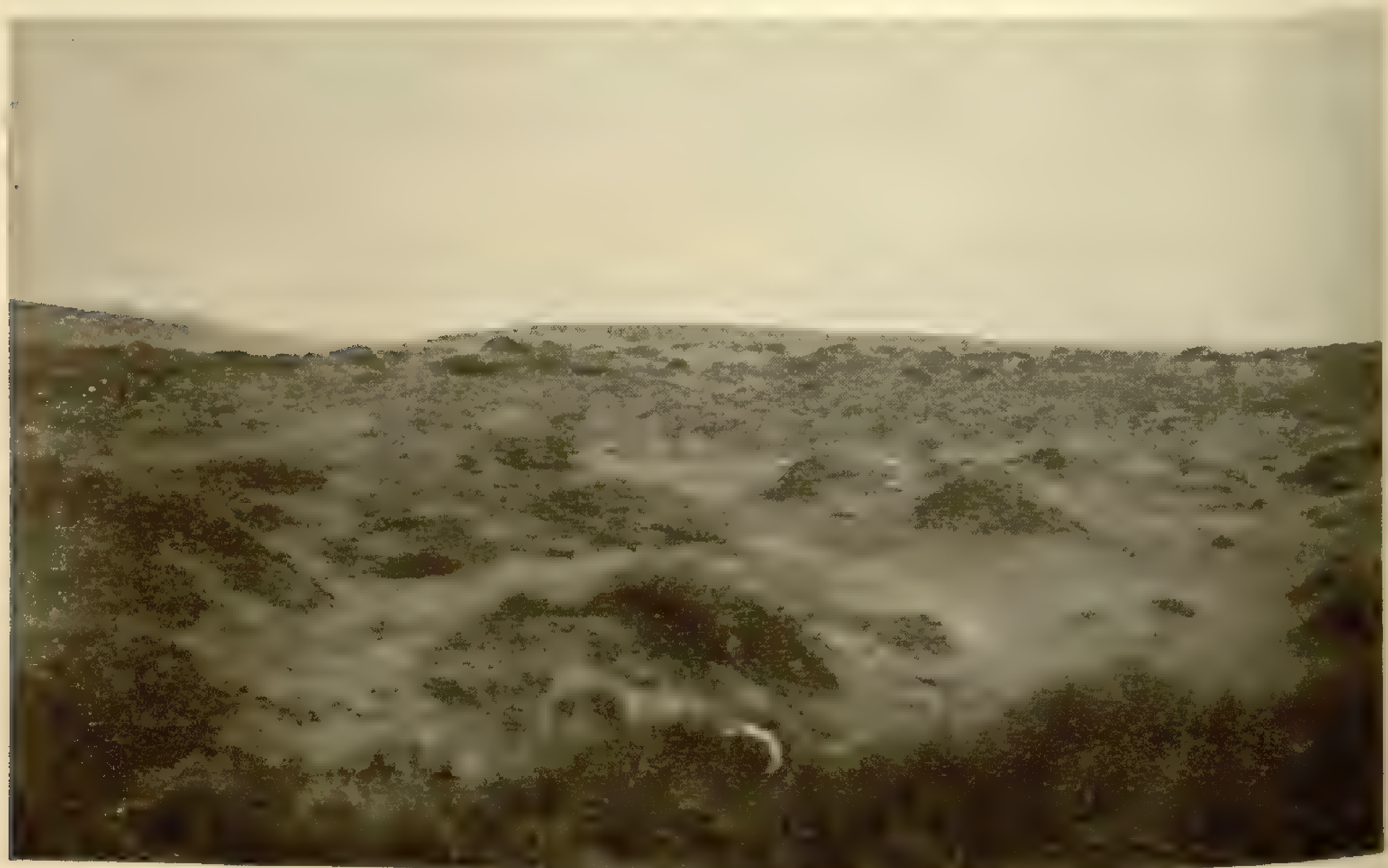

FIG. 3.—Embryonic dunes inland from littoral dune, south of Cliff House, San Francisco, Cal. (Photograph by author.)

Vegetation covering on the ground will greatly slacken the speed of the air current which comes into immediate contact with the ground, and if bushes or other obstructions are in the path of the wind, dunes are often formed behind them (*fig. 3*). The plants that are first struck by the whole force of the wind are mostly injured, not only by its mechanical action, but to a greater extent by the sand carried by the wind. While the wind in itself dries the plant, the sand particles, which often have a high temperature, are still more apt to increase the evaporation, and thus to hinder the development of the plant (*fig. 4*). Further, stems of plants growing on exposed places on coastal sands are often eroded by the sand, and even the green leaves are sometimes cut into shreds during severe storms by the sharp angular sand grains.

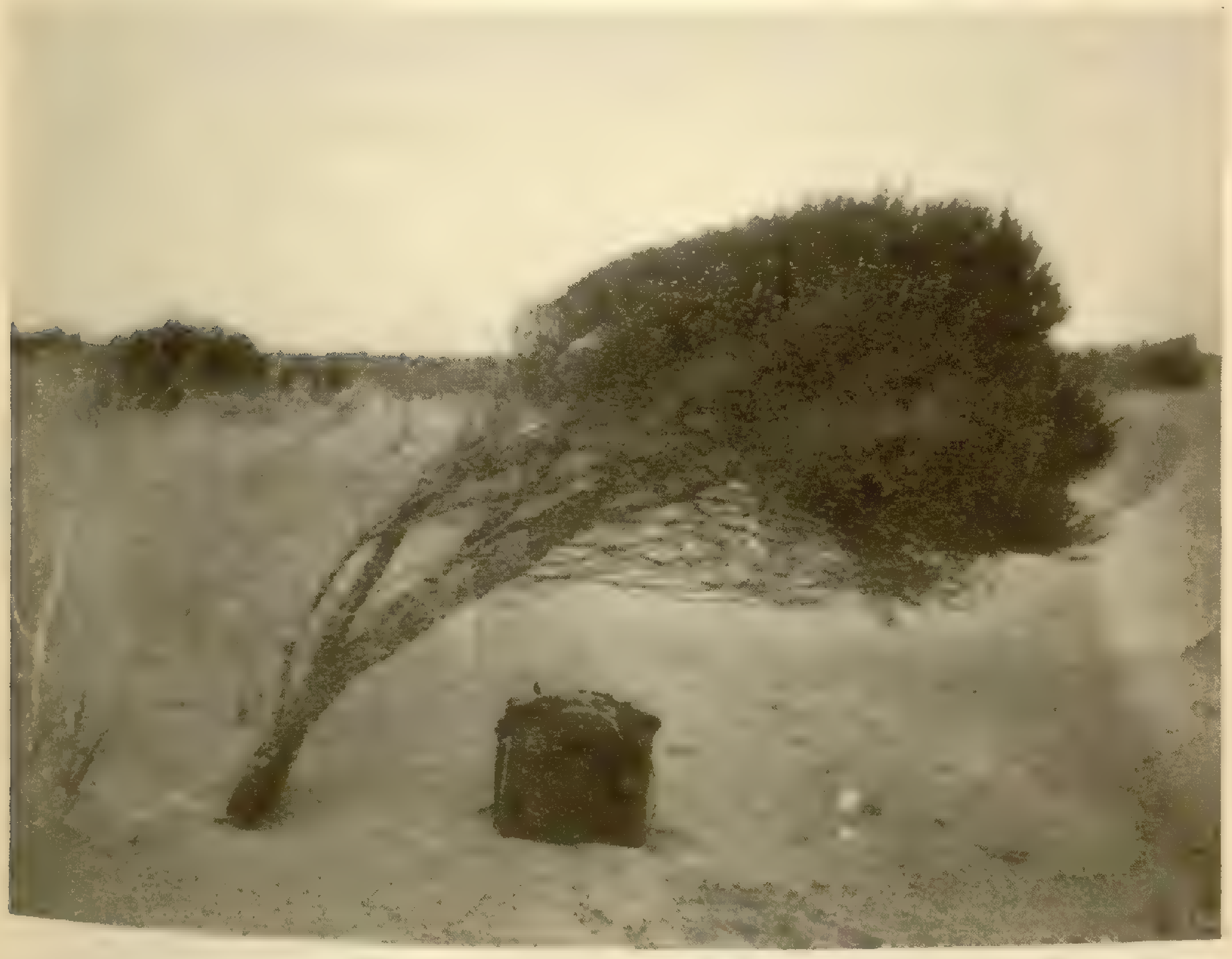

FIG. 4.—Effect of wind on *Leptospermum scoparium* Forst. on dunes at New Brighton, Canterbury, New Zealand. (Photograph by Dr. L. COCKAYNE.)

OTHER SEDIMENTS.—As we have pointed out in another place sand is especially likely to accumulate in the neighborhood of river mouths, and in such places heavy floods often carry down and deposit on the sand considerable quantities of mud, which then enrich the soil, and cause the appearance of a quite new flora, that soon will exclude the true sand plants.

On almost all marine coasts quantities of seaweeds are thrown ashore by the waves, but in warm climates they are so rapidly decomposed and the remains washed away, that no accumulations can be effected. In more temperate regions, however, these seaweeds lie in banks on the beach for some time, and add to the fertility of the soil. *Figs.* 5 and 6 show such kelp banks from the coasts of New Zealand and West Australia.

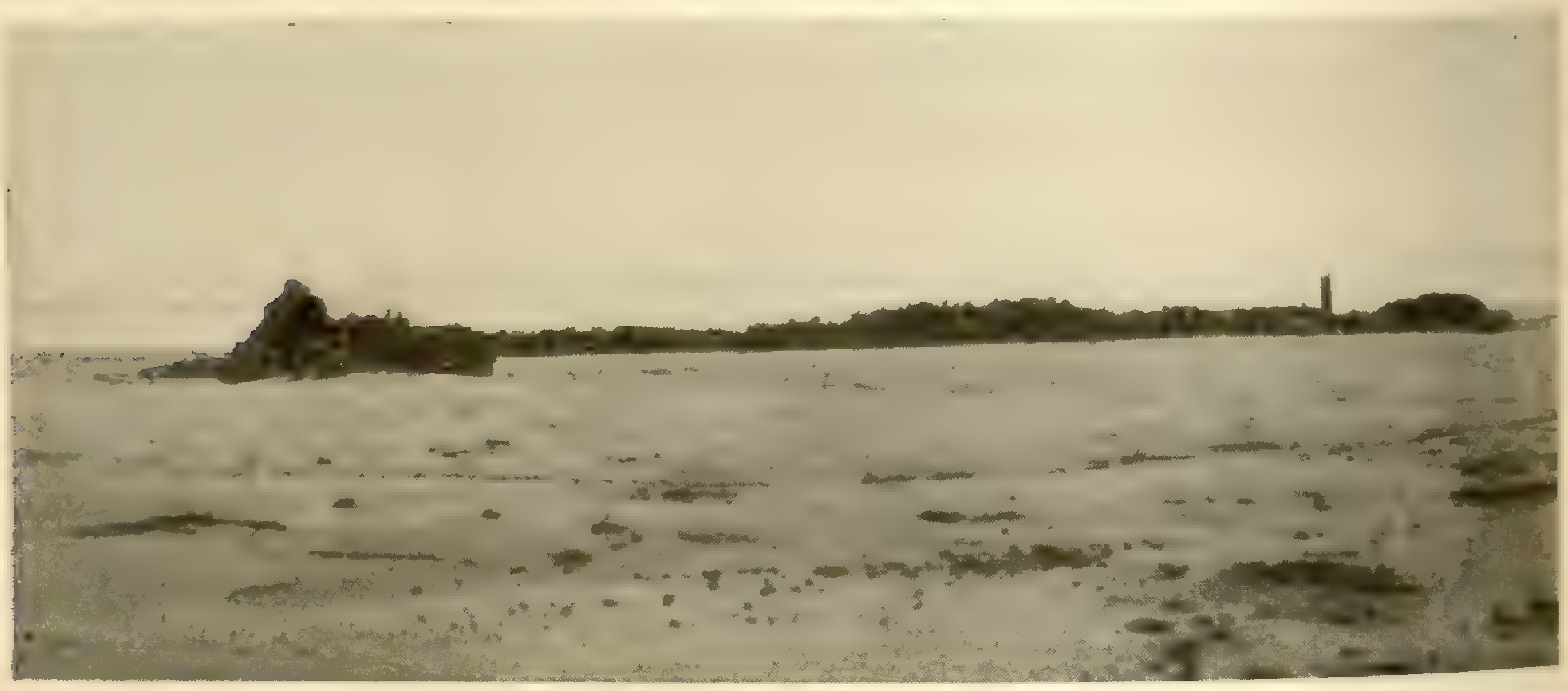

FIG. 5.—Bank of Macrocystis on the beach at New Brighton, Canterbury, east coast of South Island of New Zealand. Height of scale 41 cm. (Photograph by DR. L. COCKAYNE.)

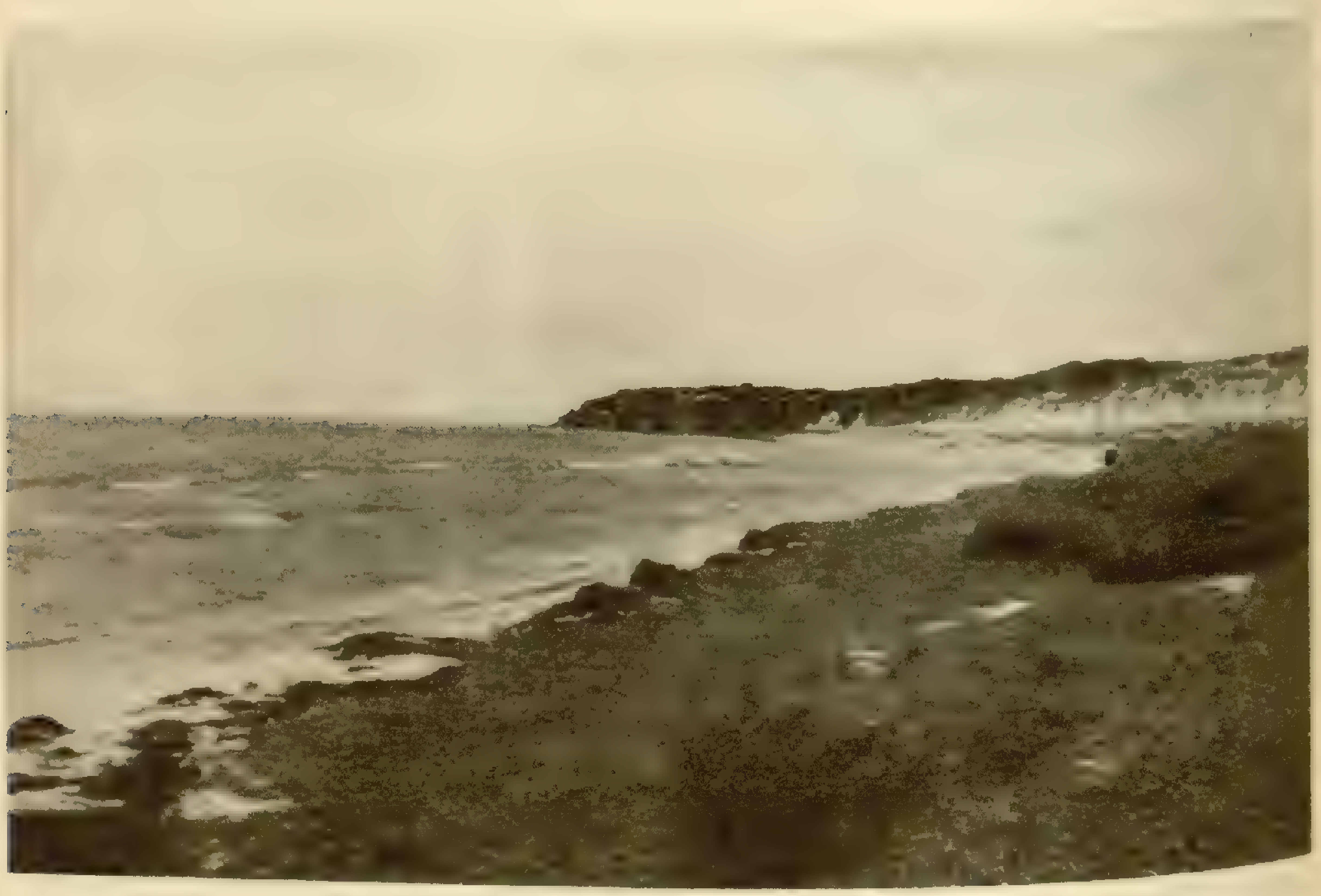

FIG. 6.—Kelp banks on West Australian coast. (Photograph by author.)

Along the shores of the Baltic a considerable amount of seaweeds, principally *Fucus vesiculosus*, is deposited on the beach at high-water mark. On open shores these banks mark the limit of vegetation toward the sea, and are characterized by a vegetation quite different from that on the rest of the beach.

MAN'S INTERVENTION.—The principal influence of man on coastal sand floras is a result of his endeavors to arrest the drifting of sand. This is mainly done by planting so-called sand-binding plants, or by covering the loose sand with refuse or other material. Either action brings about a considerable change in the natural development of the sand vegetation.

Near cities the sand dunes are sometimes used for supplying sand for industrial purposes, and in such cases the removal of the sand will naturally change the conditions for the original vegetation. Fires are sometimes started through the carelessness of man, but as the natural vegetation is very seldom dense, the influence of fires on sand formations on the coast is not great, except in artificial plantations.

Grazing animals do more injury to the sand vegetation by trampling and uprooting the plants than by actual feeding on them, and in the neighborhood of many cities, where sandy beaches and dunes occur, human agency is equally detrimental to the plant covering.

Summary

Summing up the physical conditions prevailing on the various sand formations on marine coasts we would say that *the submerged beach* is always covered with water, and therefore is the most salty of all the formations. The soil is loose, the temperature that of the sea water, and the surf is continuously beating. The vegetation is therefore especially adapted to these conditions, and in most cases no plants at all are able to gain a footing on this formation.

The front beach is periodically washed by the waves, presenting alternating terrestrial and aquatic conditions. It is almost constantly exposed to the spray and has a salty ground not very deep under the surface. The soil is very loose, still more so than on the submerged beach. Strong insolation, rapid evaporation, and a constantly changing temperature are characteristic. It is on account of these adverse conditions usually devoid of vegetation, with the exception of a few unicellular algae, often Cyanophyceae, but where the formation has not been inundated for a few days only the spores of the algae retain their vitality. On the Baltic coasts where the salinity of the sea water is low, conditions approach more or less those on fresh-water shores, and many green algae occur in the sand. The width of the barren front strand varies not only with the slope, but also with the force of the surf.

When a higher vegetation occurs on this formation it is open and very poor. The loose soil, the wind, and the impact of the surf place a limit on the types that are able to develop. These are mainly annuals or perennials with long creeping rhizomes and the flora is always poor both in species and individuals.

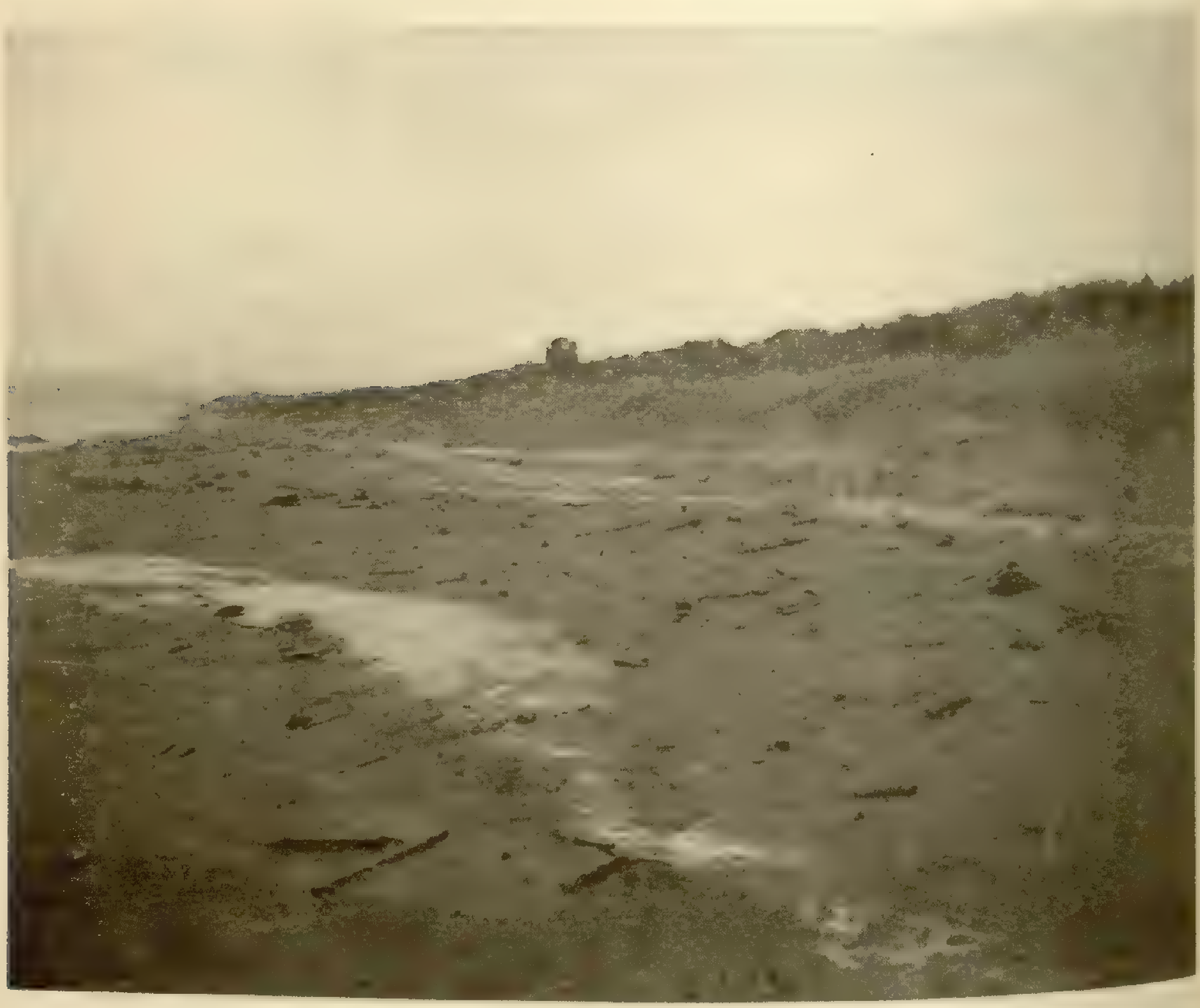

FIG. 7.—Middle and upper beach south of Cliff House, San Francisco, Cal. On upper beach small dunes made by *Cakile americana*. In background littoral dune with Ammophila. (Photograph by author.)

The middle beach is characterized by its light color, its abundant moisture, its low salinity, its loose soil, and its comparatively low temperature. Occasional inundations, spray, and wind are the direct causes of the scattered vegetation, consisting mainly of annuals or a few perennials. These plants also are more or less dwarfed, because of the wind and the cold substratum. The tension line between this and the following formation is very marked. Some-

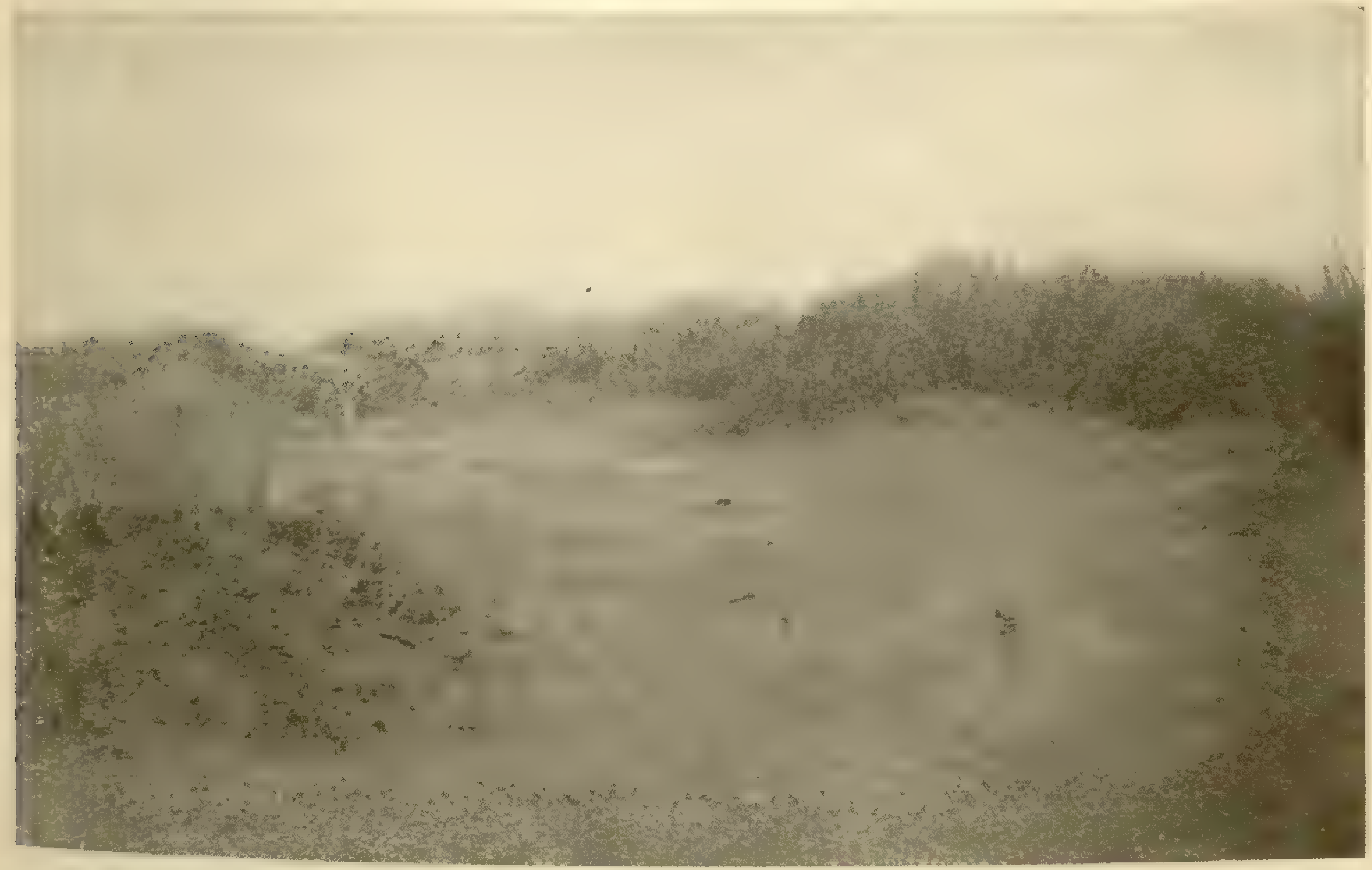

FIG. 8.—Ammophila dunes at San Francisco, Cal. Embryonic Salix dune to the left. In winter. (Photograph by author.)

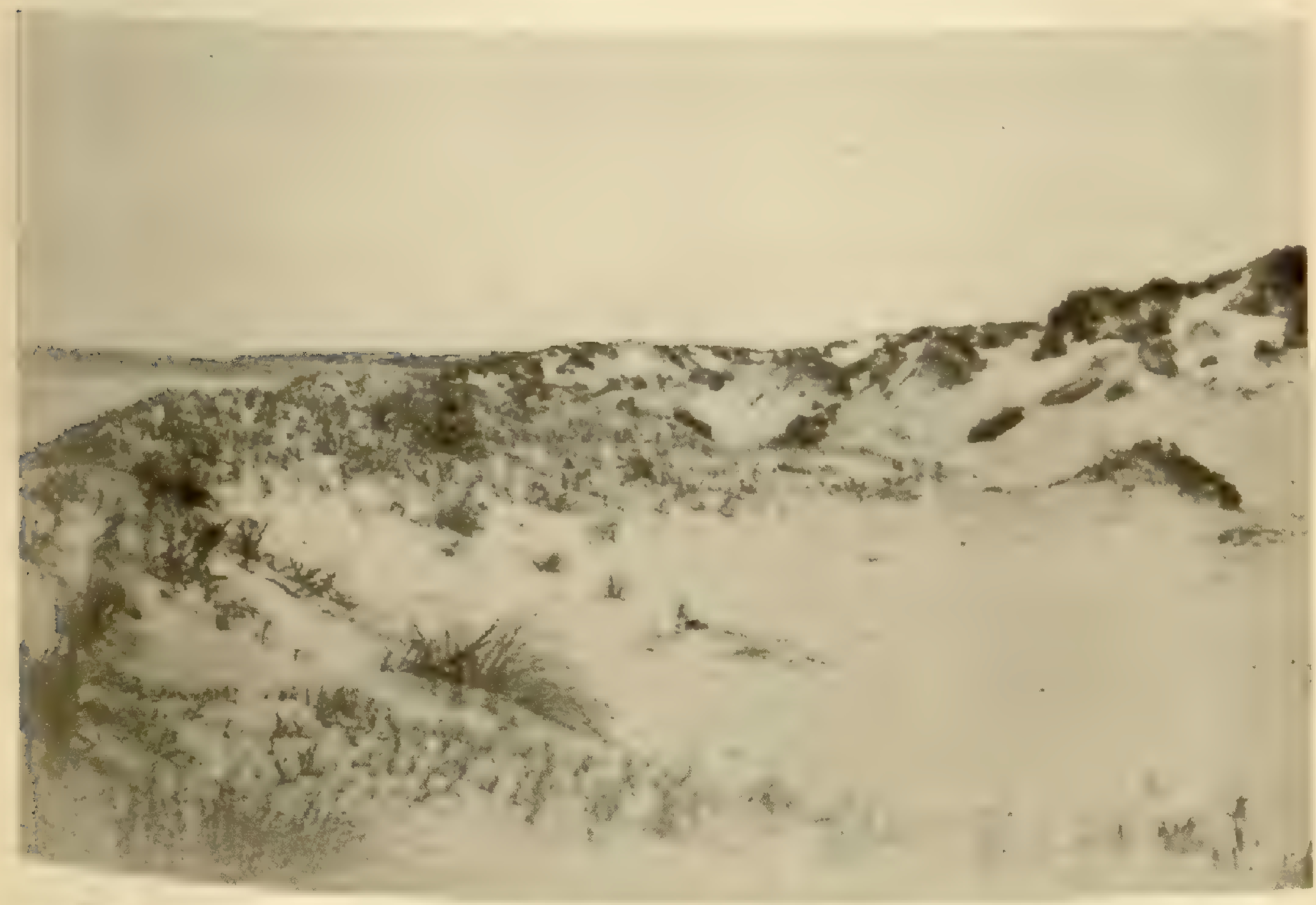

FIG. 9.—Grassy littoral dune, north of Fremantle, Western Australia. (Photograph by author.)

times a transition belt can be distinguished, marked by a darker strip of humus-mixed sand, and covered with a denser vegetation (*fig. 7*).

The upper beach has a higher percentage of humus, abundant moisture, and a higher temperature than the middle beach. The illumination is much greater, especially during certain times of the day, when the formation is not shaded by the littoral dune. Evaporation and radiation from the soil, however, are less intense, because the ground is well covered with plants. The amount of spray is less the farther we go from shore, and complete inundations occur only at very long intervals. The distance to the salty ground water is considerably greater than on the lower formations, and very few true halophytes appear on this belt. The influence of wind is very marked in that sand is blown from the middle beach over this formation, which often is covered with small embryonic dunes (*fig. 8*). The wind favors transportation of seeds and shoots from the middle

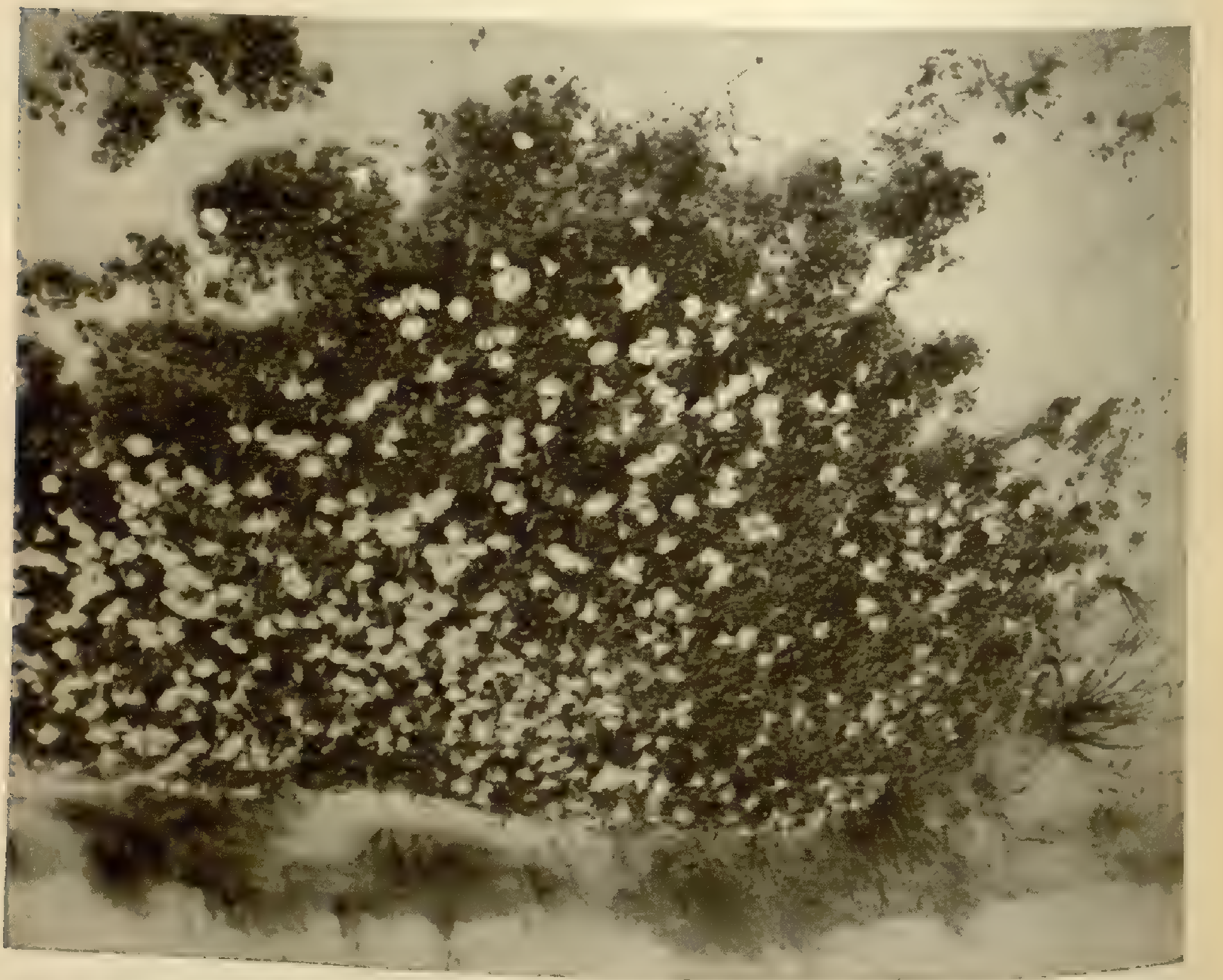

FIG. 10.—Soldanella community on dune slope at New Brighton, Canterbury, New Zealand. On summit, *Scirpus frondosus*. (Photograph by Dr. L. COCKAYNE.)

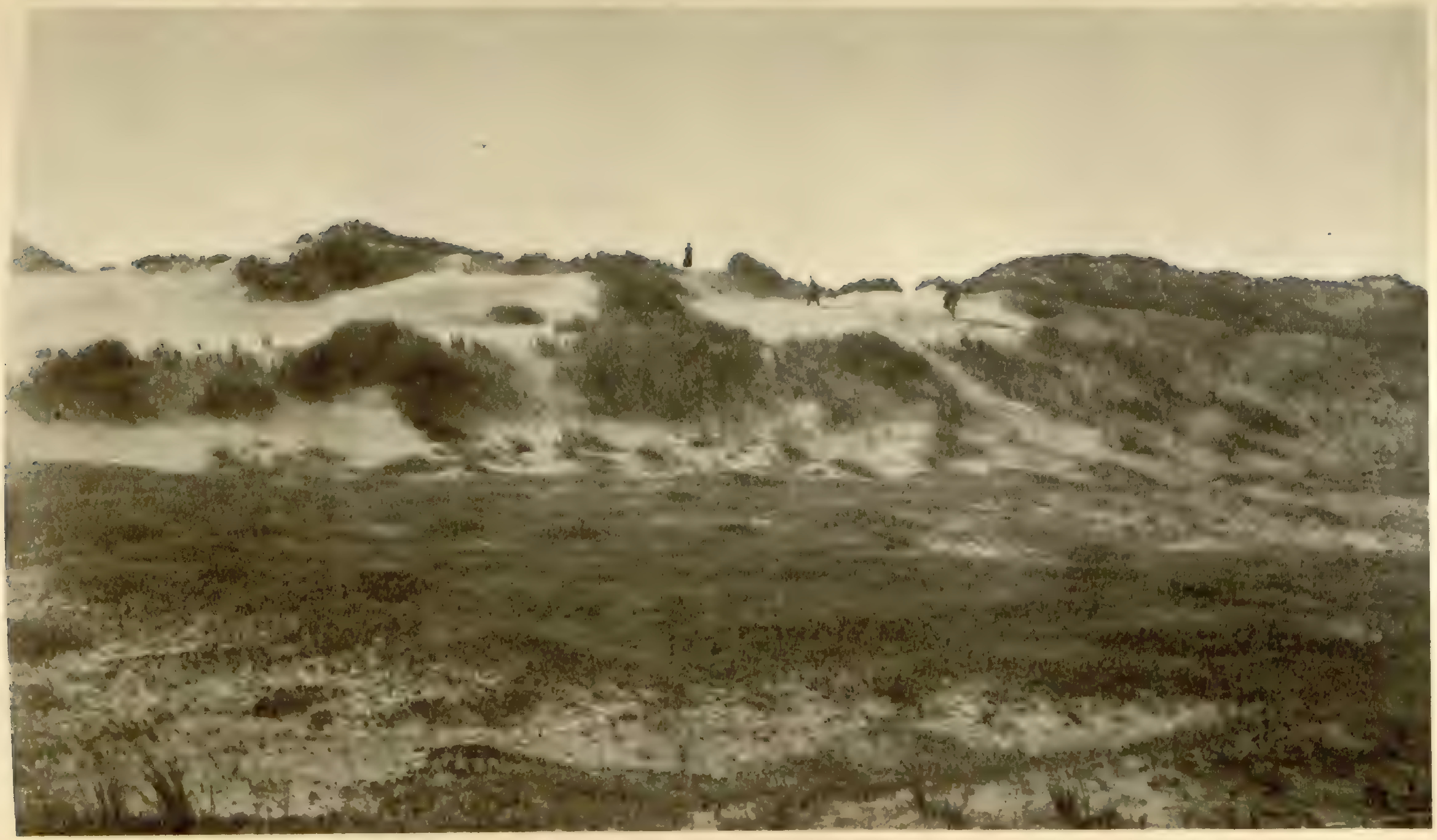

FIG. 11.—Sand dunes at Studeli Mile in north Jutland, Denmark, covered by *Elymus arenarius, Ammophila arenaria, Carex arenaria*, etc. In the foreground especially *Salix repens*. (Photograph by Dr. F. BÖRGESEN.)

beach, and in many cases the occurrence on the upper beach of plants belonging to the middle beach can only be explained by their having been blown landward from the original position.

The vegetation on the upper beach consists principally of perennial herbs, shrubs, or low trees. The tension line toward the littoral dune is not so marked as in the direction of the middle beach, but where no dune formations are developed the upper beach usually borders upon a forest. In the latter case it often happens that inland plants have wandered out to the sea-shore formations, while it never happens that sea-shore plants have been able to establish themselves inland on the meadow or forest that usually follows the strand formations.

The littoral dune is much exposed to the wind, its moisture content is low, constant oxidation of organic water goes on, and the temperature is lower than on the upper beach, because of more intense radiation. The soil is very loose, shifting, and sterile (*fig. 9*). The vegetation shows the results of these conditions very plainly. It is prostrate and dwarfed in habit, scattered and poor in variety of forms.

The active dune (the white dune of WARMING) has all the characteristics of the littoral dune in excess, and its vegetation is generally still more monotonous. Some difference can be observed in regard to the plants on the slope and summit of the dunes. It is usually richer in species on the latter part of the formation.

The stationary dune (the gray dune of WARMING) is formed at a greater distance from the sea, where the sand has to some extent consolidated, and a heather vegetation has been established. Formation of humus goes on, the plants grow closer and closer, mosses or lichens occupy the ground between the higher plants, and finally the soil is completely covered with a carpet of vegetation. This heather association is the final stage in the series of sand-plant communities beginning on the small embryonic dunes to leeward from the littoral dune (*fig. 11*).

The sandy field is richer in humus than any of the former sand formations mentioned. It has a comparatively level surface, is better able to retain moisture, and has a higher temperature. The sand grains are of such uniform size as to prevent ripple or dune formation, and

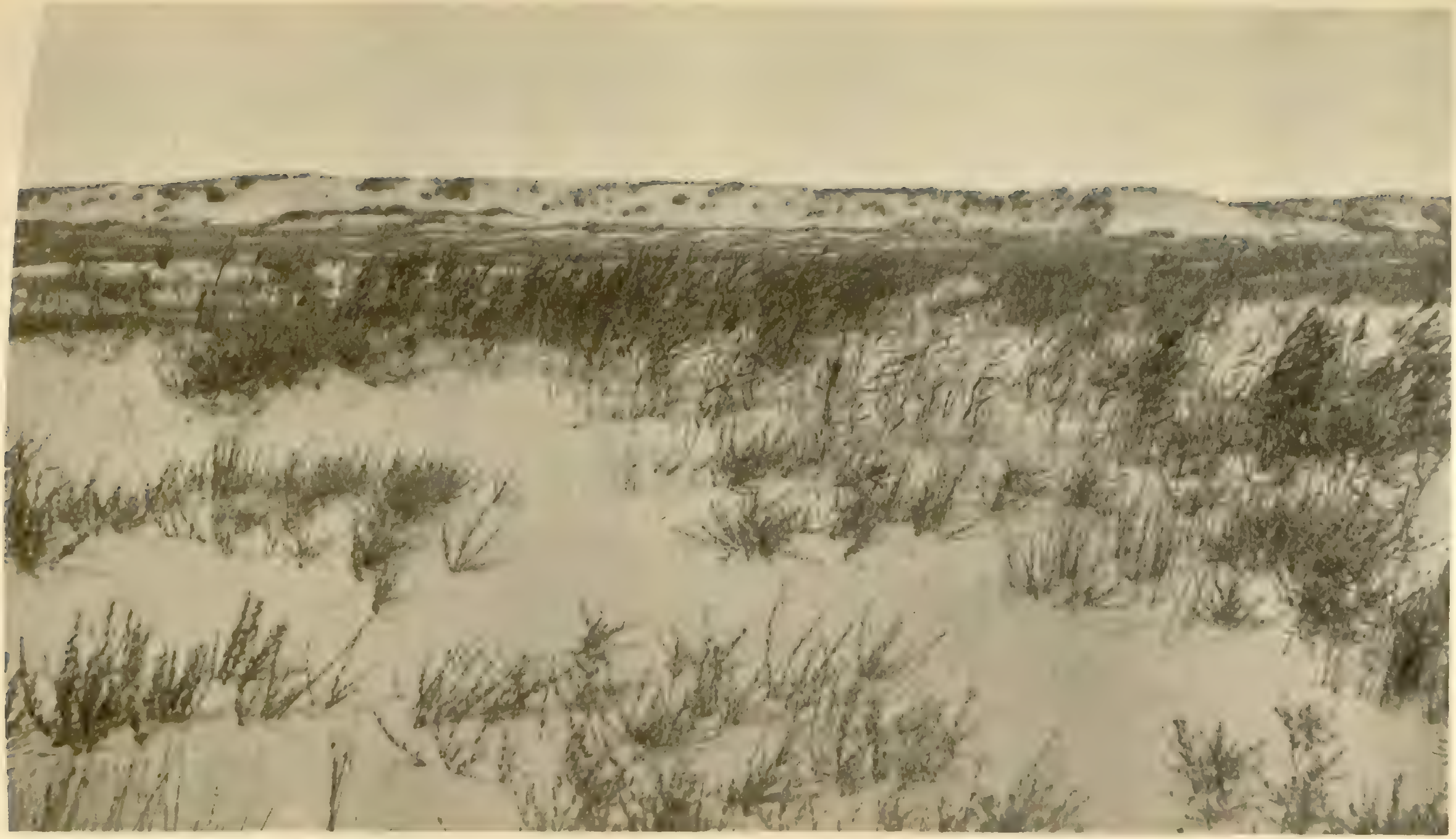

FIG. 12.—Sand field at Lodskovvad Mile in north Jutland, Denmark. The place was formerly a shallow lake, which had been filled in with sand three years previous to the time (August 18, 1898) when the picture was taken. The vegetation consists of *Salix repens*, *Juncus balticus*, *Agrostis alba maritima*, *Eleocharis palustris*, and *Phragmites communis*. In the background sand dunes with Elymus and Ammophila. (Photograph by Dr. F. BÖRGESEN.)

the vegetation covering is consequently developed in quite a different way from that on dunes (*fig. 12*).

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SOME ASPECTS OF AMITOSIS IN SYNCHYTRIUM[1]

ROBERT F. GRIGGS

(WITH PLATES III AND IV)

Previous papers on the cytology of Synchytrium have announced very striking peculiarities in the nuclear behavior of this interesting fungus. The idiosyncrasies, only a portion of which have yet been described, are so abundant at a certain period of the life-cycle of the plant that it is very difficult to consider any one set of phenomena without quickly becoming involved in all the rest, either because of the occurrence of different types of structures in the same coenocytic cyst, or because of transitional forms apparently connecting diverse structures. While no final interpretation of any one series of nuclear transformations can be made until it has been brought into relation with the whole life-history, it is apparent that it is out of the question to work out all of the peculiarities at once. The present paper is an attempt to isolate and describe one of the most conspicuous groups of nuclear phenomena. Further correlation of this with other manifestations of nuclear activity will be undertaken in later papers.

As in the preparation of a former paper on Synchytrium (GRIGGS 7), the writer is under very great obligations to his friend, Professor F. L. STEVENS, for the information which aroused his interest in the problem and for criticism of the results. This obligation is increased by the fact that Dr. STEVENS also supplied the material from which the slides were made. The present paper deals entirely with one species, *Synchytrium decipiens* Farlow. The drawings have all been taken from preparations stained with Heidenhain's iron alum hematoxylin. The triple stain has also been used.

In the cytology of this plant there is no more striking feature than the variation in the size of the nuclei. In the same cyst nuclei are frequently found ranging all the way from 8 or 10 μ down to 1 μ in diameter, as was first reported by STEVENS (**12**, *fig. 2*). Very often the small nuclei are bunched together, either in a close morula-like cluster (*fig. 33*) or in a looser group (*fig. 18*). The origin and fate of these small nuclei is the subject of the present paper. Although such variations in the size of the nuclei are sometimes found in almost any stage of the period of nuclear division, they are most conspicuous immediately after the division of the primary nucleus and continue prominent until there are 200–300 nuclei in the cyst. It is at this same stage that the other peculiarities in the cytology are most pronounced. While this period of irregularities is not sharply marked off from the succeeding phases of the life-history, yet as the nuclei become more and more numerous there seems to be a tendency for them to settle down, so to speak, and to conform more nearly to the usual habits of dividing nuclei in growing tissue.

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[1] Contributions from the Botanical Laboratory of the Ohio State University, No. XL.

The isolation of these groups suggests that their constituent nuclei have a common origin. Because of the absence of any pairing, and because of their great differences in size, one is inclined to suspect that they have been derived by some process other than mitosis. Since mitosis in this plant is always simultaneous, involving all the nuclei in a cyst, the differences could not be due to the failure of some nuclei to divide, while their neighbors became smaller and smaller by repeated division. They might of course be due to some process of mitosis in which the products were unequal, as in the reduction division of an animal egg. But all the mitoses observed gave rise to equal daughter nuclei. Further, mitoses in cysts of this age are uncommon. This led STEVENS (**12**) to suggest the possibility of an amitotic origin for the nuclei of this stage.

There are several processes of direct nuclear division in Synchytrium. Two of these are quite different from the commonly observed division by an amoeboid constriction of the parent nucleus. While they may be considered under the general term amitosis, which has come to include several forms of non-mitotic division, they require distinctive terms for their designation. Indeed, there is considerable need for a classification of the different forms of direct division, especially in view of the increased importance amitosis is likely to assume in future cytological discussion. The first process, which consists of a budding-out of a small nucleus from a larger, may be designated *nuclear gemmation*. The second differs from ordinary amitosis in that the nucleus loses its membrane and vacuole of karyolymph before the division, which is a multiple fragmentation. This form of division I shall term *heteroschizis* (ἕτερος, different, and σχίζειν, to split).

NUCLEAR GEMMATION

In nuclear gemmation, as is usual in amitosis, the division of the chromatin is not nearly so frequently observed as the separation of the two nuclei. In the resting nuclei of Synchytrium the whole of the chromatin content is usually concentrated in a single globular karyosome (nucleolus). At the beginning of nuclear gemmation the margin of this karyosome becomes crenate, and rounded lobes develop, which separate from it and become smaller independent karyosomes (*figs. 4–8*). Sometimes only one daughter karyosome migrates from the parent at a time (*fig. 6*); sometimes the parent undergoes a process of bipartition resulting in equal daughter karyosomes (*fig. 7*); or sometimes several form at once, in which case the whole karyosome breaks up (*fig. 4*). *Fig. 8* shows a very large nucleus where the daughter karyosomes were unusually numerous. They were not free in the nucleus, as appears from the drawing, but all of them were lying against the nuclear membrane, only one hemisphere of which is represented.

After the separation of the small karyosomes is complete, *they migrate through the nuclear membrane.* This process is probably rather gradual, since all stages are easy to observe: *figs. 8, 19* show them lying loosely against the membrane; in *figs. 9, 20* they are pressed against it; in *figs. 8, 21* they have begun to pass through; *fig. 21* shows one lying almost exactly half-way through the membrane; *figs. 10, 11* show karyosomes which have passed through, but still lie close against, the membrane.

As soon as the passage is completed, a vacuole, similar to the cavity of the parent nucleus, appears around the migrating karyosome. This is quickly surrounded by a membrane, extending out from the wall of the parent nucleus into the cytoplasm next the vacuole (*fig. 10*). This process can be observed satisfactorily only when the daughter nucleus is of considerable size, because of the delicacy of the membranes of the smaller nuclei. When the membrane is complete the new nucleus moves away from the parent and becomes an independent small nucleus free in the cytoplasm. The stages in this process are also easy to follow: *figs. 3, 9, 11* show cases where the karyosome is still in contact with the membrane of the parent; *figs. 6, 12, 13, 18* cases where the karyosome has separated from the parent, but the membranes remain in contact; *figs. 3, 5, 9, 14* cases where the two nuclei have separated, but still lie close together.

Division by nuclear gemmation occurs also in the spirem stage (*figs. 15–17*). In this case the division of the chromatin takes place at the time of spirem formation and cannot be definitely connected with nuclear division, but the manner of the separation of the daughter nuclei is the same as that already described. *Figs. 1, 2* show groups of small nuclei from a cyst where all the large nuclei (*fig. 16*) are in spirem.

In cysts where the nuclei are numerous and evenly scattered through the cytoplasm it can be seen that the peripheral nuclei divide much earlier than the central ones. Groups of small nuclei are always found at the periphery before the large nuclei in the center are much divided. Thus a lateral section of a cyst (*fig. 1*) shows only uniform groups of small nuclei, while the central sections show numerous large nuclei, of which *fig. 16* is an example.

Nuclear gemmation may take place at very different rates in different cysts. In the cyst from which *figs. 11, 12, 14* were taken, the few small nuclei present are scattered singly through the cytoplasm. In this case the appearances indicate a slow and orderly formation of small nuclei. In other cysts the chromatin seems to be extruded with almost explosive violence (*figs. 24–26*, cf. also GLASER **6**). In these cases a large proportion of the migrating chromatin never forms nuclei but degenerates in the cytoplasm. Some members of almost every large group are imperfect and disintegrate, forming in their last stages deeply staining spots in the cytoplasm. Such disintegration is seldom seen in cysts where the small nuclei give evidence of more gradual formation. It is more pronounced in younger cysts where there are only a few parent nuclei, than in later stages where they are numerous.

The deeply staining granules on the nuclear membrane vary from karyosomes half the size of the mother karyosome to microsomes similar to those usually found in the nuclear membrane in both animal and plant cells (*figs. 7, 18, 21, 22*). No optical distinction can be drawn between these extremes. The very smallest granules, however, do not form small nuclei but may function in metabolism. In mitosis and in the degeneration of the large nuclei (*fig. 22*) they are cast aside with the old nuclear membrane and lost in the cytoplasm. But no distinction can be drawn between these granules and those which form small nuclei, for some of the latter are excessively minute. Besides these, there are yet other granules on the nuclear membrane from which conspicuous radiations proceed into the cytoplasm as from centrosomes (*fig. 39*). The discussion of these bodies involves other questions than those considered in the present paper and cannot be undertaken here. Another complicating factor is the frequent presence of asters near nuclei which are giving off gemmae. I have avoided using such cases for the figures of the present paper, but in many instances nuclei adjoining those drawn had conspicuous asters, and it would be possible to duplicate most of the drawings herewith given from nuclei showing asters. But though the centrosome problem, one aspect of which was touched in a former paper (GRIGGS **7**), is very puzzling and far from solution, my belief is that it is independent of the phenomena discussed in the present paper.

HETEROSCHIZIS

The second process of amitosis is a multiple division or fragmentation of the nucleus, which occurs for the most part at later stages than nuclear gemmation, but is sometimes found in young cysts (*fig. 33*) and rarely also even in segmented cysts (*fig. 34*). Nuclei derived by heteroschizis are at once distinguished from those due to nuclear gemmation, because they form not a loose group but a close morula-like cluster, as figured by STEVENS (**12**, *fig. 3f*). As in nuclear gemmation, all the stages in their formation are easy to observe and may be found in a single cyst. But while the new nuclei are formed one at a time in that process, here they originate simultaneously by the fragmentation of the mother nucleus. The first indication of division consists in the loss of the nuclear membrane and the vacuole of nuclear sap, leaving the karyosome lying naked in the cytoplasm, like the chromosomes in the metaphase of mitosis (*fig. 27*). The karyosome then apparently enlarges to nearly double its former size (*fig.*

28). This statement is based on the fact that the naked karyosomes are, in the cases observed, larger than those of any other nuclei in the same cysts, and that the resultant clusters of small nuclei are greater in mass than any single nucleus in the cyst at this stage. The variation in the size of the nuclei, however, is so great in other stages that it is not impossible that these may have been larger nuclei in the beginning. Lobes (*fig. 29*) now appear on the margin of the karyosome, each of which rounds off and becomes the karyosome of a small nucleus. When these karyosomes have separated, vacuoles of nuclear sap appear around them; surrounding membranes are next formed in the meshes of the cytoreticulum bounding the cavities, thus completing the process. The membranes, however, do not appear simultaneously around all the nuclei of a cluster. There is usually sufficient difference to allow some observation of the process of membrane formation. The vacuoles which become the nuclear cavities are at first indistinguishable from those between the meshes of the cytoreticulum which are filled with cell sap, but they are gradually surrounded by membranes which are apparently precipitated from the cytoplasm next the cavity. Neither in heteroschizis nor in nuclear gemmation is there evidence of any connection of the centrosomes with membrane formation such as occurs in the reconstruction of the nucleus after mitosis (KUSANO **8**, GRIGGS **7**).

Besides the two sorts of amitosis just described, a third method has been observed a few times. In this process, which has been seen only when the nuclei were in spirem, the nucleus becomes strongly lobed; each lobe contains a portion of the original unchanged spirem; the lobes become more pronounced and are cut apart by continued constriction. There may be only two lobes, as in ordinary amitosis, or there may be several, as in heteroschizis. Although even a single nucleus of this kind (*fig. 40*) would seem to indicate the general nature of the process, there is much concerning it which is doubtful, and its occurrence is rare in my slides. I refrain, therefore, from more than mention of the matter at this time.

LATER HISTORY OF THE SMALL NUCLEI

If amitosis leads to degeneration and death, as has been held almost universally until recently, we should expect to find a large percentage of degenerating small nuclei in every cyst where they occur, either during the period of their formation or later. After nuclear gemmation, however, degeneration of chromatin is relatively small in amount and is almost altogether confined to masses which never organize nuclei. It occurs not in the later portion of the period of gemmation but only during the early portion, when there are few large nuclei in the cysts. In clusters due to heteroschizis, degeneration may also occur at later stages, but is infrequent at any time. If, on the other hand, these amitoses are due to pathological conditions affecting the whole parasite, we should expect to find a large number of dying cysts. Fully three-fourths of all the few-nucleate cysts give evidence of amitosis. Of the remainder only a small number show mitoses at this stage. This hypothesis would therefore require that three-fourths of the cysts should degenerate sooner or later. But no such thing occurs. Degenerating cysts are seldom found, and the degeneration gives no indication of being connected with earlier amitoses.

The clusters of small nuclei arising from heteroschizis tend to remain close together, and when mitosis is resumed they may form a cluster of small spindles. *Fig. 35* shows such a cluster between prophase and metaphase, in which the remains of the nuclear membranes are still evident. Below them is the solitary spindle of a large nucleus, of which there are 40–50 in the cyst. *Fig. 36* shows three objects from another cyst assembled in one drawing. At *a* is a similar cluster of small spindles; at *b* is one of the solitary spindles of the larger nuclei, all of which in this cyst are in a later phase than the clusters; at *c* is a deeply staining mass which has the appearance of a cluster similar to *a* degenerating. *Figs. 37, 38* show similar clusters in anaphase. Although the spindle fibers in *fig. 38* are distorted so as to give somewhat the appearance of a pathological multipolar spindle, some of the spindles are perfectly normal. The spindles of *fig. 37* resemble closely the solitary spindles of the cyst and are typical examples of the peculiar anaphases of this genus.

The groups of small nuclei arising by nuclear gemmation scatter quickly, so that there is no means of connecting them with the mitoses which occur later. They have the usual relations, however, to the cytoplasm and appear normal in all microscopic characters. When not too small they bud off other small nuclei in the same manner (*fig. 18*). This process usually continues till all the nuclei in the cyst are approximately equal in size (*figs. 1, 2*). Sometimes all the daughter nuclei given off are so much smaller than the parent that the mother karyosome is never divided up among the daughters, but remains behind full size, after giving up its chromatin, like the nucleolus in the prophases of mitosis. In this case the *large nuclei* degenerate and leave the small ones as the functional nuclei of the cyst. *Fig. 20* shows the first indication of this in the vacuolate karyosome of the parent nucleus. In *fig. 21* all the chromatin has migrated from the old karyosome but some of the small karyosomes still remain inside the nuclear membrane. The larger of these are about the same size as the numerous small nuclei of the cyst. *Fig. 22* shows another large nucleus from the same cyst, which is entirely bereft of chromatin. *Fig. 23* is the last stage of the process; here the old nuclear membrane has disappeared and the faintly staining old karyosome (nucleolus) lies naked in the cytoplasm. Beside it is shown one of the functional nuclei. We are therefore led to the conclusion that the nuclei derived by these processes of amitosis are normal, and that they with their descendants become the functional nuclei of later stages, capable of perpetuating the species.

GENERAL CONSIDERATIONS

Although the processes by which these nuclei are derived are novel, the formation of normal tissue by amitosis is by no means without parallel. C. M. CHILD (1–5) has recently shown that amitosis is a frequent occurrence in regenerating organs, embryos, and in some adult animals. He records instances from most of the great animal phyla, including coelenterates, flat worms, trematodes, cestodes, insects, amphioxus, fishes, amphibia, and birds. In these cases, contrary to what would be expected, there seems to be no especial distinction between the soma and the germ plasm as to the origin of the nuclei. In Moniezia, a tapeworm infesting sheep, which CHILD has worked out most fully, the germ plasm is almost exclusively derived by amitosis and the spermatogonia may even undergo a sort of amitotic reduction by which sperms are formed without ever having passed through mitosis. In general, amitosis is most common in regions of excessively rapid growth, where the nuclei are small and have scant cytoplasm, while the larger nuclei, better supplied with cytoplasm, divide by mitosis. This leads CHILD to conclude (**5**, p. 292): "In short I am inclined to believe that amitosis is associated with conditions where the demand for material or perhaps for some particular substances exceeds the supply." The behavior of the nuclei of Synchytrium is distinctly opposed to the generalization of this hypothesis, for in Synchytrium amitosis is most marked when the nuclei are largest and the ratio of nuclei to cytoplasm is at a minimum. While a condition of "hunger" may very well be assumed to exist in the cells of a rapidly regenerating organ or in a growing embryo, it cannot be ascribed to a dividing cyst of Synchytrium, because growth is very slight after the division of the primary nucleus, while the supply of nutriment from the host is presumably as great as before.

But in all of these cases the conditions of growth demand an excessively rapid multiplication of nuclei, and indicate that the process of nuclear reproduction is pressed on so rapidly as to give no opportunity for the rhythmic pause occasioned by mitosis. If the stimuli to growth and reproduction are independent, as many observations indicate, we may suppose that when the stimulus to division becomes excessive the nucleus divides directly, without waiting for the long preliminary pause necessary in mitosis. If the stimulus were but slightly stronger than in mitosis, a slow and orderly division of the chromatin would result, and the daughter nuclei would be mostly perfect; but if the stimulus became greater the process would be accelerated, until finally the nucleus would explode and a large proportion of the chromatin would never succeed in forming new nuclei at all. This is exactly in line with CHILD'S view that amitosis is an orthodromic process which ". . . . pushed to the extreme must always result in the total destruction of the original substances," so that "it is not strange that degeneration frequently follows amitosis, but there is no reason for supposing that it must always follow, and the facts prove that it does not." While this hypothesis may not cover cases of pathological amitosis, which superficially would seem to accord with the hunger hypothesis, it would afford a basis for associating the non-mitotic divisions in Synchytrium with those in regenerating members, embryos, and other rapidly growing tissues.

Knowledge that in certain instances the reproductive cells of a species are independent of mitosis for their origin must affect current theories of heredity, which, since the renaissance of MENDEL'S law, have leaned very heavily on the individuality of the chromosomes and their separation in the reduction division. CHILD rejects the chromosome theory in any universal application. He believes (p. 290) that "these processes appear to consist essentially in the production of new nuclear material like that already present and without the periodical recurrence of metamorphosis. The act of division is very probably a mere incident of the increasing volume of substance." Accordingly he is inclined to doubt the constancy of the chromosome number in the tapeworm, although he feels that the facts are too difficult of determination to admit of certainty. In Synchytrium, likewise, the minuteness of the nuclei makes determination of the chromosome number so difficult that one hesitates to dogmatize. But in all the many cases in which the chromosomes could be counted on the spindle the number seemed to be constantly four (cf. *fig. 36b*). The same number was given provisionally by STEVENS (**13**) in his first paper and is shown by the drawings of his second paper (**12**). This matter may, however, be left for consideration later, after the mitoses have been worked out in detail. But whether the chromosome number is found to be constant or variable, it is obvious that our theories of heredity will require considerable revision.

SUMMARY OF RESULTS

The numerous peculiarities in the cytology of Synchytrium occur mostly in a somewhat definite *period of irregularities* immediately following the division of the primary nucleus.

In this stage direct division of the nucleus is more frequent than mitosis. This takes place by at least two processes:

1. *Nuclear gemmation.*—The karyosome of the parent nucleus gives off a small karyosome which migrates through the nuclear membrane, forms a vacuole and a membrane about itself, and becomes an independent small nucleus, the whole looking like a budding yeast plant. This process is repeated until the parent nucleus is converted into small nuclei, often forming a definite group.

2. *Heteroschizis.*—The membrane of the parent nucleus dissolves,

and the karyosome fragments into a number of pieces, each of which becomes a new nucleus, thus giving rise to a morula-like cluster of nuclei.

These nuclei at later stages undergo mitosis and their descendants form spores and become the nuclei of succeeding generations.

No variation in the number of chromosomes in any of the nuclei of the plant has been detected.

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EXPLANATION OF PLATES III AND IV

The figures were all made with a Spencer 1.5^{mm} immersion objective and compensating ocular 12, giving a magnification of 2130, excepting *fig. 1*, for which ocular 2 (magnification 355) was used. They were reduced ⅓ in reproduction, canceling the enlargement due to the camera and rendering them the same size as they were seen in the microscope.

PLATE III

FIG. 1.—A lateral section of a cyst, showing numerous groups of small nuclei due to nuclear gemmation.

FIG. 2.—One of the groups shown in *fig. 1*.

FIGS. 3–6.—The breaking-up of the mother karyosome preparatory to the migration of the chromatin.

FIG. 7.—Bipartition of the mother karyosome to form equal daughters.

FIG. 8.—Nucleus with a large number of daughter karyosomes lying on the nuclear membrane, only one hemisphere of which is shown.

FIG. 9.—A nucleus with one of the daughter karyosomes pressed against the nuclear membrane; three small nuclei which have budded off from it near by.

FIG. 10.—Daughter karyosome constructing its nuclear cavity and membrane.

FIG. 11.—Daughter nucleus complete but still closely appressed to the membrane of its parent.

FIGS. 12, 13.—Karyosomes of daughter nuclei separated from the parents but their membranes still in contact.

FIG. 14.—Daughter nucleus separated from its parent but lying close by.

FIGS. 15–17.—Nuclear gemmation from the spirem stage. (*Fig. 16* is one of the large nuclei from the center of the cyst from which *figs. 1* and *2* were taken.)

FIGS. 18–20.—Resultant groups of small nuclei.

PLATE IV

FIGS. 21–23.—Stages in the degeneration of the parent nuclei.

FIGS. 24–26.—Nuclei from which chromatin has been thrown out in large quantities and is mostly degenerating without forming new nuclei.

FIG. 27.—Beginning of heteroschizis; nuclear membrane dissolving, karyosome slightly irregular.

FIG. 28.—Membrane and nuclear cavity lost, karyosome much enlarged. Same cyst as *fig. 27*.

FIG. 29.—Karyosome lobed. Same cyst as *figs. 27* and *28*.

FIGS. 30–32.—Karyosomes broken up, nuclear membranes appearing around the daughter karyosomes. (*Fig. 32* is from the same cyst as *figs. 27–29*.)

FIG. 33.—A very large cluster complete.

FIG. 34.—A single segment from a summer sorus whose nucleus has divided by heteroschizis.

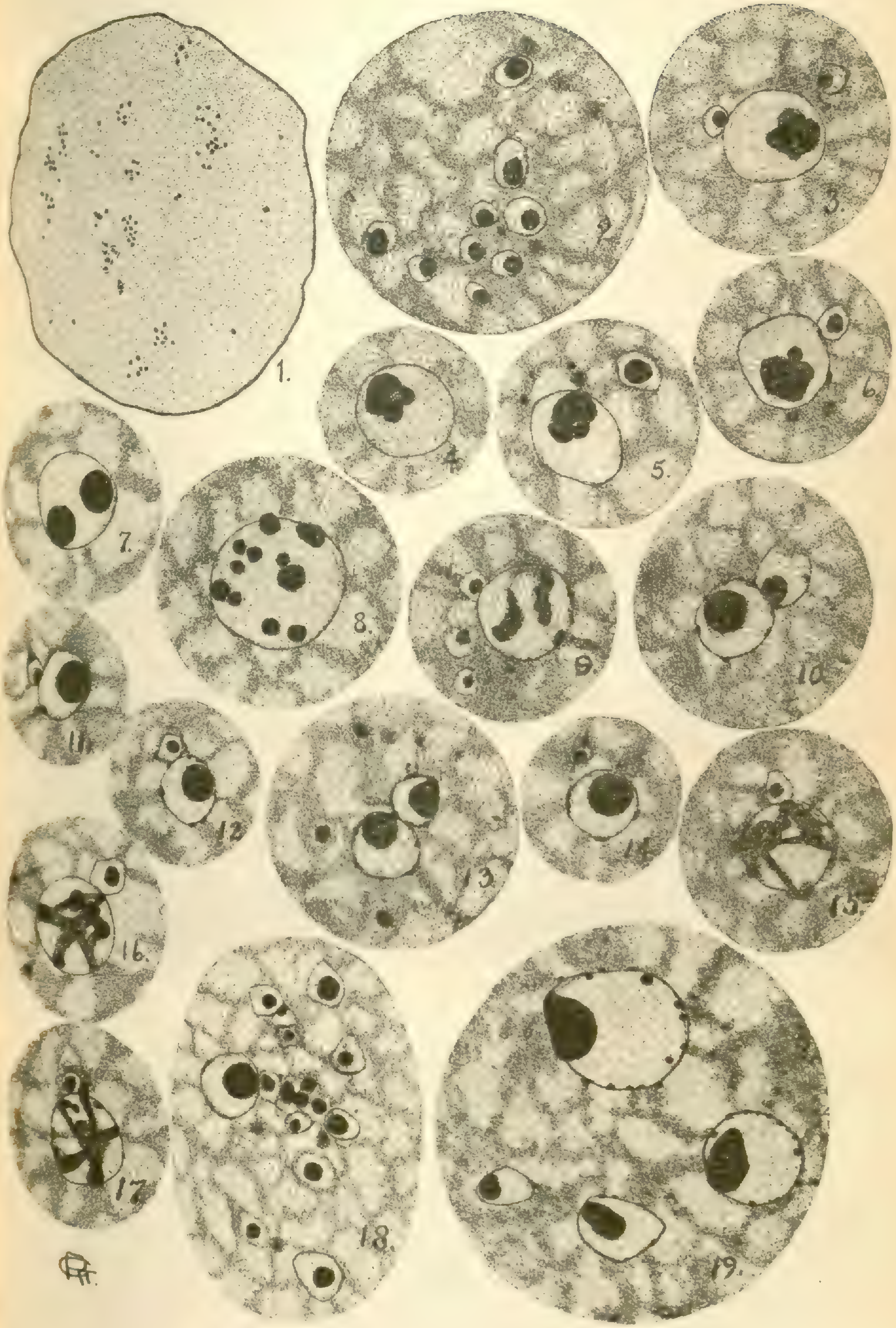
FIG. 35.—A cluster of spindles arising from the division of such a cluster as *fig. 33*, together with a single spindle of one of the solitary nuclei of the cyst.

FIG. 36.—*a*, a cluster of spindles similar to *fig. 35*; *b*, a solitary spindle from the same cyst; *c*, probably a cluster of spindles disintegrating.

FIGS. 37, 38.—Similar clusters of spindles in anaphase.

FIG. 39.—A nucleus with deeply staining granules on its membrane, from which radiations are given off into the cytoplasm.

FIG. 40.—A nucleus fragmenting by constriction.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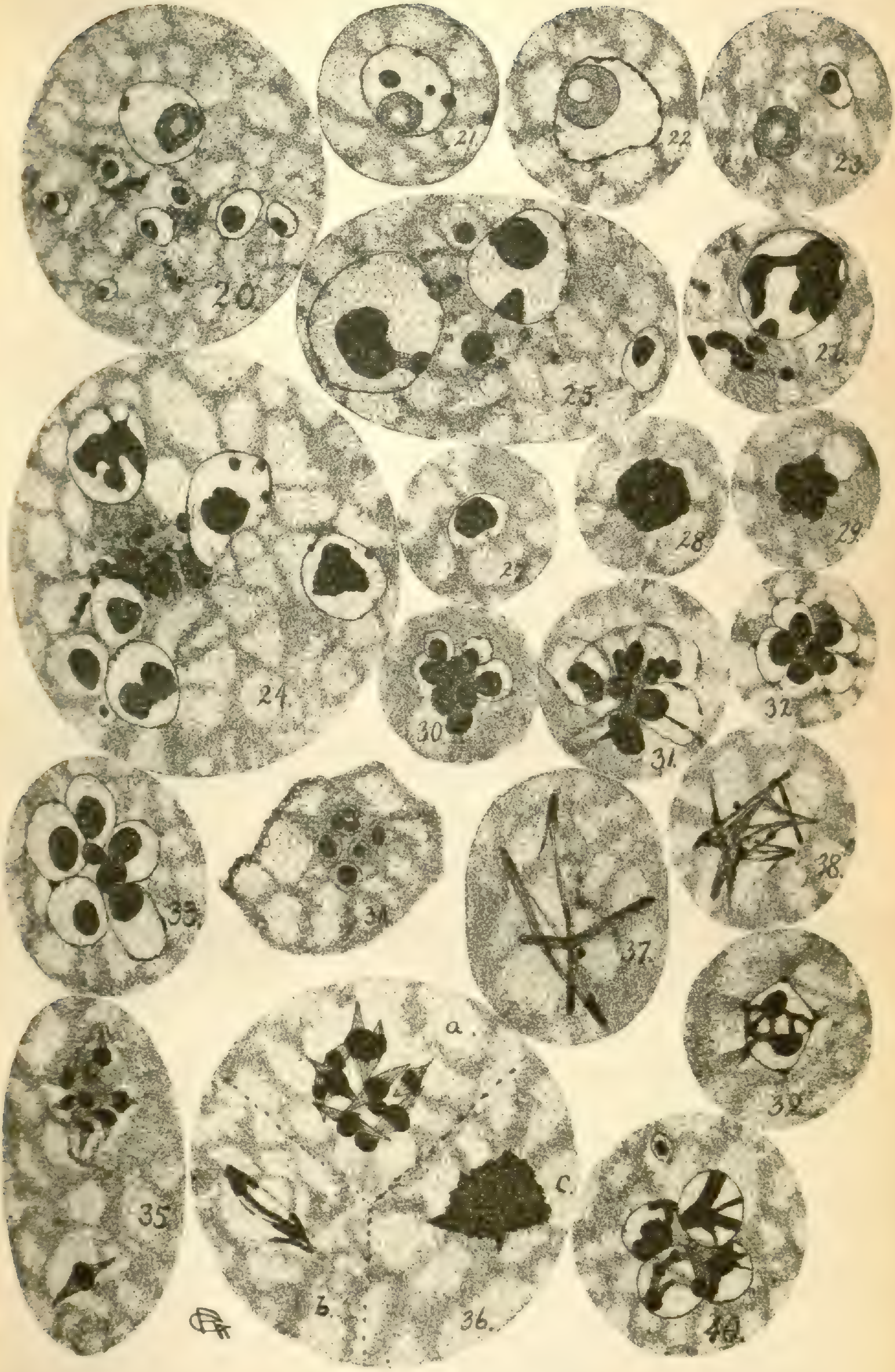
GRIGGS on SYNCHYTRIUM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GRIGGS on SYNCHYTRIUM

VASCULAR ANATOMY OF THE SEEDLING OF *MICROCYCAS CALOCOMA*

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 122

HELEN ANGELA DORETY

(WITH PLATES V AND VI)

HISTORICAL

DECANDOLLE (5) in the first account of the genus Microcycas expresses the opinion that it holds a position among cycads intermediate between Dioon and Zamia.

A historical sketch of the literature concerning *Microcycas calocoma* may be found prefacing the taxonomic account of the species by CALDWELL and BAKER (1), who succeeded in procuring material from Cuba. The only part of their description which concerns us here is the statement that the stem has a single vascular cylinder.

In a second paper, intended primarily to present the conditions in the reproductive structures, CALDWELL (2) has described incidentally some of the superficial characters of the embryo and seedling. Certain details, which he naturally overlooked in so comprehensive a work, have been brought to light by a more detailed study having the seedling alone as its object.

INVESTIGATION

In the first place, it is not the root which is seen to emerge from the seed and bend downward, as described and pictured by this author; the sequence of events in the process of germination is the same as that described for Ceratozamia (7), the same which occurs in the other cycads which I have germinated, *Dioon edule*, *D. spinulosum*, and species of Zamia. The root is not yet formed when the base of the elongating embryo ruptures the seed coat in the small, less indurated, micropylar region. When it emerges, it still bears the small brown disk constituting the only remains of the coleorhiza, an organ which, in the early stages of the embryogeny, is by far the larger portion of the sporophyte. The united cotyledonary stalks bend downward toward the soil. The root may not pierce the coleorhizal disk until the latter has touched the soil; indeed its appearance in some seeds is preceded by the exit of the plumule.

A second detail in which this description must differ from the one cited is that the usual number of cotyledons is only two. They never wholly emerge from the seed. Their common stalk, which forms a sheath about the plumule, is soon ruptured in many places by the radial growth of the latter, and its decay causes the seed to drop away.

The appearance of embryos of Microcycas, like those of Ceratozamia described by CHAMBERLAIN (**3**), examined at short intervals during the period between fertilization and germination, indicates that there is no resting stage; and if at any time the seeds are allowed to dry, the embryos are killed. LAND (**10**) relates that he has reason to suspect the same condition in Ephedra.

CALDWELL has called attention to the adhesion of embryo to endosperm. This adhesion is greater than in any of the cycads I have studied, except Zamia. So intimate is the union, that by using ordinary precautions, one does not separate them entirely, but always carries some few layers of the endosperm through the microtome and stains with sections of the embryo.

Coincident with the close adhesion of embryo to endosperm is the remarkable fusion of the cotyledons. Although these always arise as two distinct organs, the fusion in older embryos is so complete that several were sectioned from the apex to within a distance of 0.5^{mm} above the tip of the plumule without discovering any trace of the characteristic seam made by the meeting of the adaxial epidermal layers (*fig. 1*). The epidermal cells themselves disappear in many cases slightly above the meeting of the inner faces over the plumule. The seam was not seen to extend to the surface at any level in these embryos, although there were conspicuous superficial sutures (*fig. 1*) in some of them. The plumule is liberated by the splitting of the sheath into strips, each of which simulates the petiole of an individual cotyledon. To my knowledge so complete a fusion of cotyledons has not been reported of a cycad.

Each cotyledon may have eight or ten vascular strands; all are collateral, with normal orientation. Apparent exceptions may occur immediately above a dichotomy or immediately below a fusion or an approximation. In these situations, the xylem of one strand faces that of the other, giving to the inner one an inverse orientation (*d, figs. 1, 2*). When the fusion of two bundles is complete, the combination presents the appearance of a single concentric strand.

All the cotyledonary traces are derived from the branching of three, which join the central cylinder (*fig. 3*) in a manner similar to that described by MATTE (**11**) and THIESSEN (**12**) for *Dioon edule*, and by the present writer (**7**) for Ceratozamia. The wood remains endarch as far out as the sheathing base of the cotyledons (*fig. 13*); it becomes mesarch in this region; and in the upper portion of the blade the wood in the greater number of the strands is exarch. Transfusion tissue is abundant, and in close connection with the centripetal xylem. Mucilage ducts alternate with the cotyledonary traces. Tannin cells are conspicuous in the peripheral region.

The hypocotyl has no vascular plate, no protostele; the passage from stem to root is therefore easily studied. The four cotyledonary strands remain distinct throughout this portion of the axis, only fusing laterally with the few elements of the leaf traces still remaining to form a very imperfect siphonostele. Their elements finally unite with those of the four root poles. The metaxylem and phloem divide, as usual, and the resulting portions swing to right and left, the right half of the phloem of each joining with the left half of that of the next, with sometimes the lowermost extremities of leaf-trace phloem intervening (*fig. 4a*). There is thus produced the characteristic root structure, four groups of phloem alternating with four double-fan-shaped xylem groups. Irregular proliferation of the medulla often separates the phloem group again into its two constituents (*fig. 6*).

In the cortex of the hypocotyl were discovered the remains of a very broken zone of cambium. No traces, however, of any vascular tissue could be detected outside the central system in seedlings with two expanded leaves and several others developing.

The root in all the seedlings under observation was tetrarch (*figs. 4a, 6*) with a reduction to triarch toward the tip, in some cases. Mucilage ducts are numerous in the hypocotyl, but do not penetrate into the root. Neither pericycle nor endodermis is distinct in these young roots. The root tip differs in no observable respect from that of Ceratozamia.

In the stem four large groups of leaf traces alternate with the cotyledonary strands, just above the cotyledonary node (*fig. 3*). Higher up (*fig. 7*), they close in, and together constitute the central cylinder of the axis. Taking a generally vertical course, these traces branch and anastomose until they reach a position so near to the growing points of leaf and stem that the vascular tissue is still procambial. In this position, even before the procambial strands from leaf and stem apex have united, the traces destined for the leaf margins manifest the phenomenon of girdling.

At first the wood of the leaf traces is endarch. *Fig. 8* represents a portion of a leaf-trace girdle, and *fig. 9* a cross-section of two vertical strands from the middle of the same leaf at the same level. *Figs. 10, 11* illustrate stages in the transition from the endarch to the mesarch condition. The wood becomes exarch at a relatively low level in some of the foliar strands, and there is considerable irregularity in different traces in this respect. *Fig. 12* is a drawing of one of the traces (*b*) in *fig. 14*, still in the region of the stipules. The other traces of the same leaf retain, at this level, a few elements of centrifugal xylem; this strand is entirely destitute of them. Further—and I have attempted to represent it diagrammatically—the wood in all the traces of this petiole is more nearly exarch than in those of the older leaf (l^2), although the section of that leaf which is here represented is higher up in the petiole than that of the younger leaf. In spite of such irregularities, however, the statement holds that the xylem is entirely centrifugal near the base of both cotyledons and leaves, and that it gradually diminishes to the vanishing point in proportion to the appearance and increase of centripetal xylem in the ascent of the cotyledonary blade and leaf petiole.

The section represented by *fig. 13* is very close to the leaf bases. It shows the increase in the number of bundles entering consecutive leaves, and also the meriphyte's gradual assumption of the Ω arrangement from the open arch of the early leaves. Transfusion tissue is present in these traces.

The strands are all collateral. Frequent branchings and approximations occur, and real fusions are common, most noticeably of those strands which are brought to the center of the meriphyte and form the flanks of the Ω. When two of these strands are fusing, the centripetal elements of both xylem groups are gradually eliminated and the protoxylem groups are therefore brought together and finally united. This common group of protoxylem, then, is surrounded by the united metaxylem, and outside of this the phloem of both bundles may almost encircle the xylem, completing the delusion of a concentric bundle (*figs. 15, 16*).

Mucilage ducts occur in stem and leaves. They sometimes extend through the petiole as far as the bases of the pinnae.

The characteristic cycad ramentum is prominent, especially upon the unfolded leaves. The hairs are one-celled. *Fig. 18* shows the tip of a young pinna bearing these epidermal outgrowths.

Tannin cells occur in the periphery of the petiole, and may extend well into the pinnae. They are in close relation with the mechanical tissue, as represented in *fig. 17*.

DISCUSSION

The suppression of one of the cotyledons of Ceratozamia illustrates one process by which the monocotyledonous condition may be reached; the fusion of these organs in Microcycas affords an illustration of another method, one in harmony with the well-known theory of Miss Sargant. Experimentation with some of the monocotyledonous dicotyledons listed by Coutler and Chamberlain (5) shows that in at least some of them the former process has taken place.

But this fusion of the cotyledons of Microcycas has a further meaning to one engaged in the study of a series of juvenile gymnosperms. The free lobing at the tips of the cotyledons in so many cycads seems to me to represent an ancestral condition of polycotyledony. Many embryos of Zamia and *Dioon spinulosum* in my collection have four to ten of these lobes, extending, in some cases, three-fourths of the length of the cotyledon. A young embryo of *Dioon spinulosum* with four cotyledons, and one of *Pinus edulis* with twelve cotyledons in four well-marked groups have a remarkable similarity. Of course, the pine cotyledons soon escape from the small, comparatively dry endosperm and thin seed coats, and develop exteriorly to their full size, which is *in toto* much greater than that attained by the two cotyledons of a cycad. But let the conditions be such as to cause in the pine seed the production of the massive endosperm and indurated coats that characterize the cycad seed; and let the cotyledons be confined within the moist endosperm until they attain their full size, with the pressure of this growth forcing them into such intimate connection with it as to cause difficulty in distinguishing between them, and bringing the tips of the cotyledonary vascular strands into intimate contact with the endosperm, a condition reported by WORSDELL for *Cycas revoluta* (**13**) and by THIESSEN for *Dioon edule* (**12**): under such pressure, the inner faces of the pine cotyledons would be very intimately united and the question naturally suggests itself, What would become of the epidermis of these inner faces?

The alternation of mucilage canals with the cotyledonary vascular strands in cycads, and its ready relation to the peculiar condition found in pine cotyledons, may be used as evidence for a theory of fusion as well as for one of splitting, as HILL proposes (**8**).

The absence of the protostele in the hypocotyl of Microcycas in contrast to the condition found in *Dioon edule* and Ceratozamia may not have any significance in the light of recent investigation. That the protostele is, in general, the most primitive condition of the vascular axis may be true; but that this structure must occur in every primitive vascular plant is, of course, not true; neither are we to regard as primitive all plants in which it is found. CHRYSLER (**4**) has found it in members of the Araceae. There are other characters, however, which seem to indicate a greater advance than that made by Cycas or Encephalartos, or even Ceratozamia. These are the single stele and the degree of elimination of the cortical cambium, which, in the cycad stems, produces this vascular tissue. However, the large proportion of centripetal wood in the foliar traces is an offsetting primitive character, which must be weighed in the same balance.

The undoubted polyspermy would seem, at first sight, to bear down the weight of evidence on this side; but it is possible that this primitive feature is a recurrence rather than a direct inheritance: what JEFFREY calls a coenogenetic, rather than a palingenetic, character. JUEL (**9**) found as many as twenty sperms in the pollen tube of *Cupressus Goveniana*, and no one can believe that Cupressus has retained this primitive feature when all the closely related genera have discarded it.

However that may be, this curious combination of characters, and the absolutely unique archegonial development, are features to be reckoned with by those who, in the future, when all the evidence is in, will be in a position to decide upon the phylogenetic place of Microcycas.

What is to be thought of the early appearance of girdling is scarcely worth saying until we learn something definite concerning the cause of girdling itself. The theories now in the field approach only remotely to the causes lying at the foundation of the phenomenon. It is probable that it may be relegated, like so many other problems, to the domain of cytology. That cell division takes place much more frequently in the horizontal than in the vertical direction in every portion of the axis is clearly evident.

SUMMARY

1. There is no resting stage in the development of the embryo of *Microcycas calocoma.*
2. The germination is hypogean.
3. The root is a delayed organ, as in Dioon and Ceratozamia.
4. There are two cotyledons as in all cycads (except, perhaps, Encephalartos).
5. The cotyledons are often fused to form one organic whole, the plumule escaping by bursting the sheath.
6. Mucilage ducts alternate with the 8–10 cotyledonary strands.
7. The cotyledonary node is similar to that of *Dioon edule* and Ceratozamia, but the vascular cylinder of the hypocotyl is a siphonostele.
8. The hypocotyl contains no cortical vascular tissue, although there are remnants of a broken-up cambial zone.
9. The vascular strands of cotyledons and leaves are endarch at base and exarch in the upper portions. The exarch condition obtains throughout most of the length of the petiole.
10. Girdling of the marginal leaf traces takes place while the tissue is procambial.
11. The root is tetrarch, but may reduce to triarch toward the tip.

Grateful acknowledgments are due to Professor JOHN M. COULTER, and Dr. W. J. G. LAND, under whom the investigation was conducted, and to Professors CHARLES J. CHAMBERLAIN and OTIS W. CALDWELL for material.

THE UNIVERSITY OF CHICAGO

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EXPLANATION OF PLATES V AND VI

The drawings were made with the aid of an Abbé camera lucida. The following abbreviations have been employed: *A*, *B*, *C*, *D*, main cotyledonary traces; *cs*, cotyledonary sheath; *cfx*, centrifugal xylem; *cpx*, centripetal xylem; *cx*, cortex; *e*, epidermis; *f*, group of leaf traces; *l*, leaf; *m*, medulla; *md*, mucilage duct; *mx*, metaxylem; *ph*, phloem; *px*, protoxylem; *r*, ramentum; *t*, tannin cells.

PLATE V

FIG. 1.—Transverse section near the middle of the cotyledons, showing their complete fusion and the large number of cotyledonary strands. ×8.

FIG. 2.—Transverse section of cotyledons 0.6^{mm} above the tip of plumule. ×8.

FIG. 3.—Diagram of stele 40 μ above the cotyledonary node.

ph
mx
px
ph
t
1
d
md
2
d
4a
mx
px
4
D
A
B
3
C
f
3a
m
ph
mx
px
6
ph
mx
px
m
mx
6a
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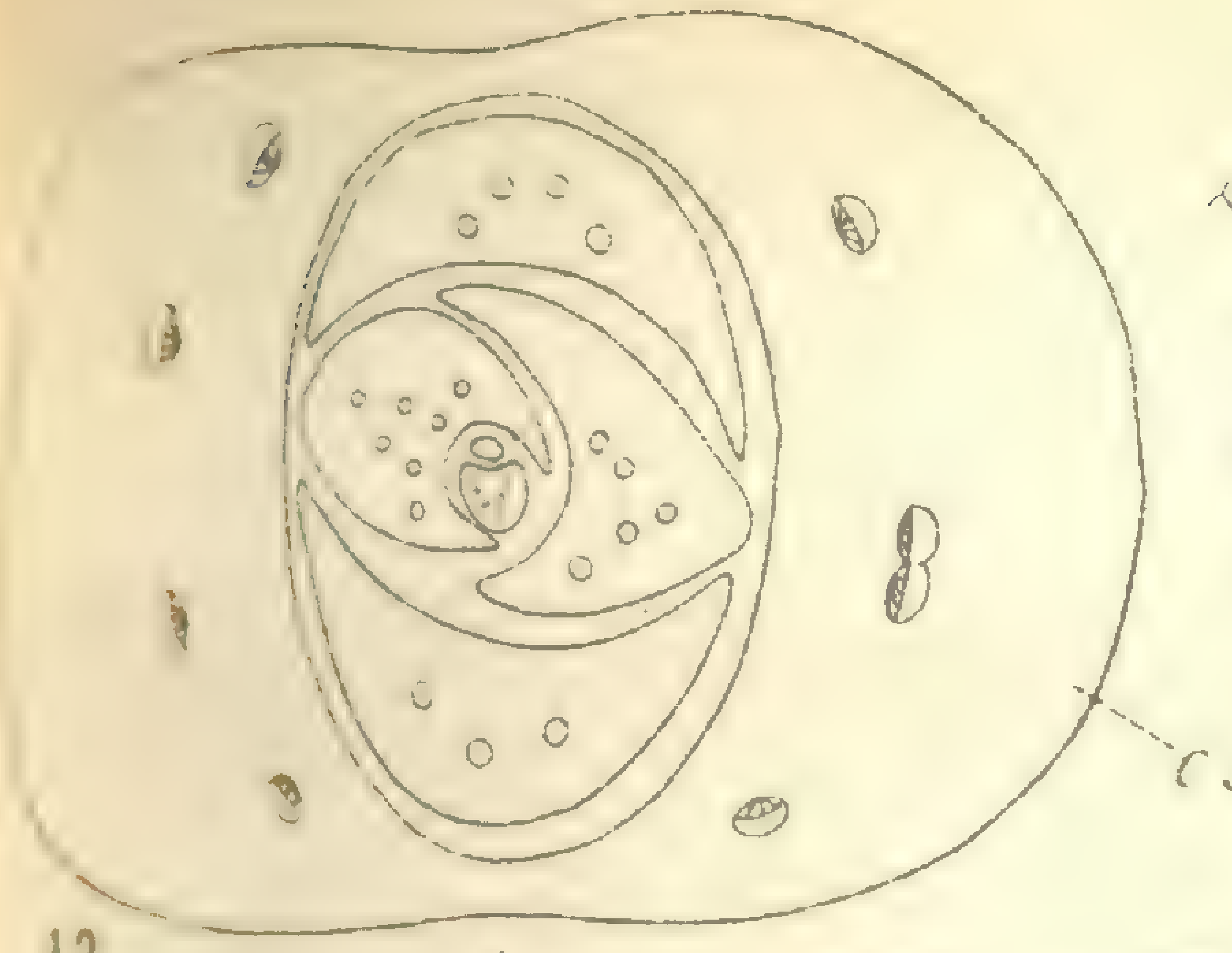
DORETY on MICROCYCAS



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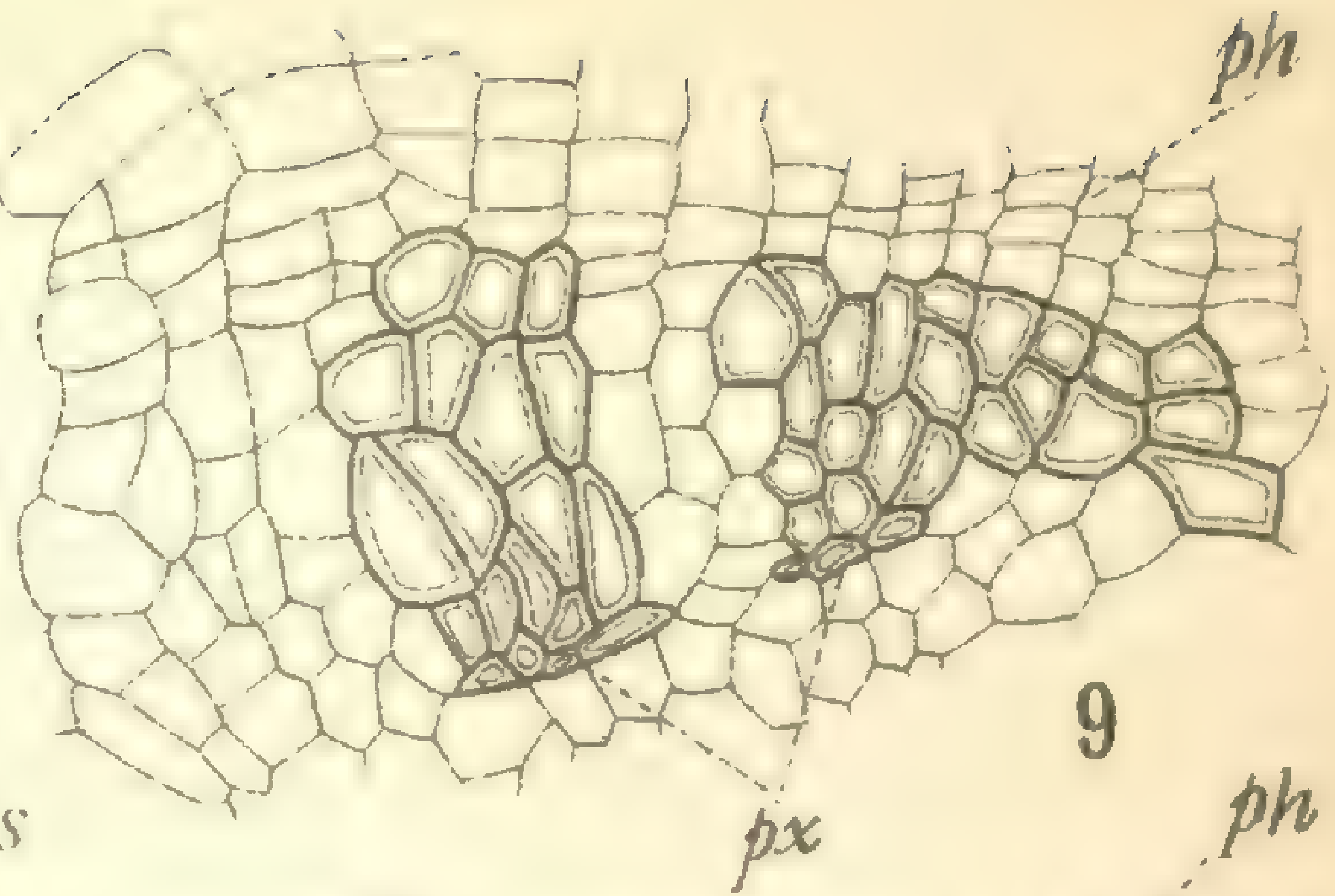

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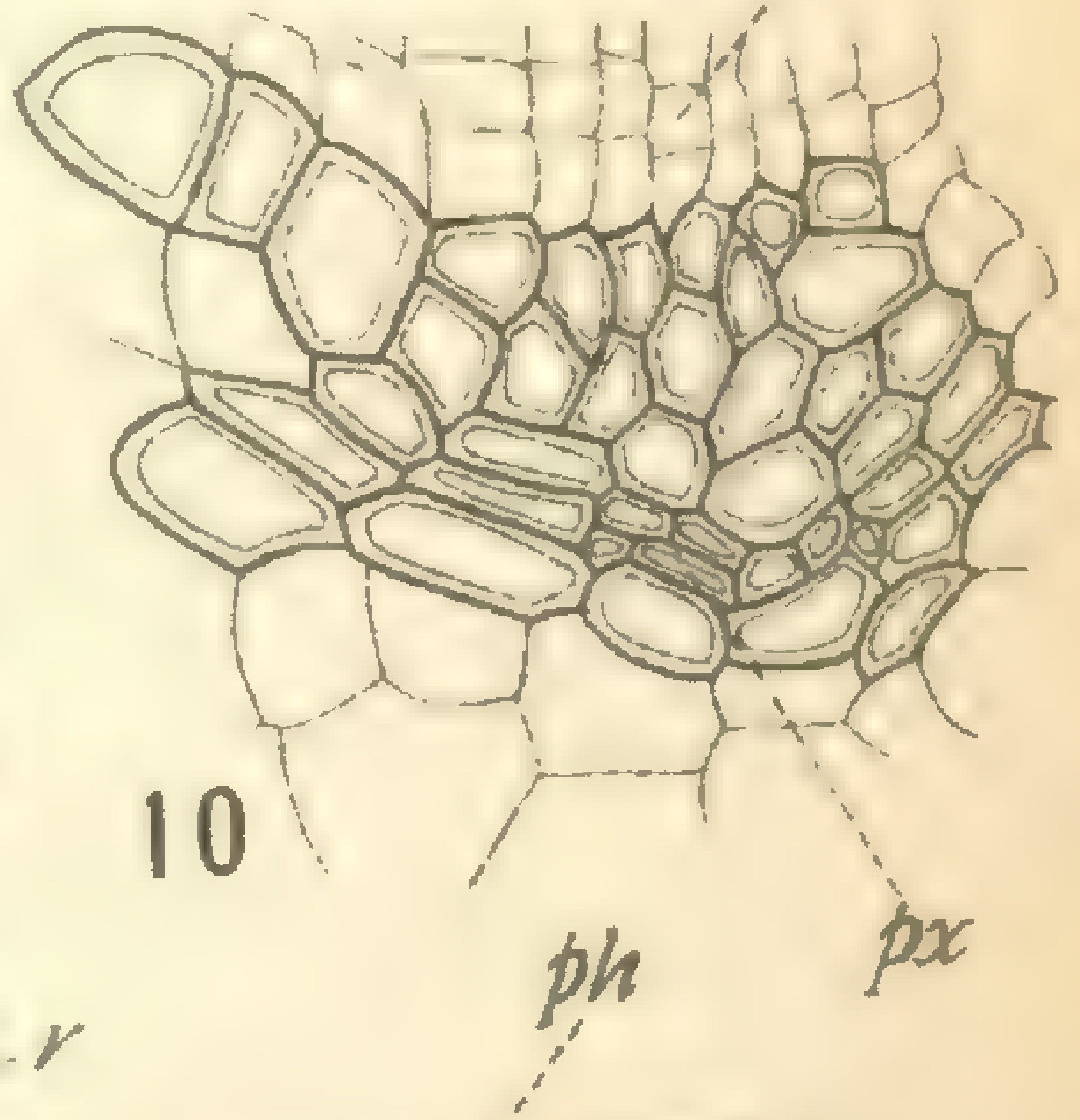

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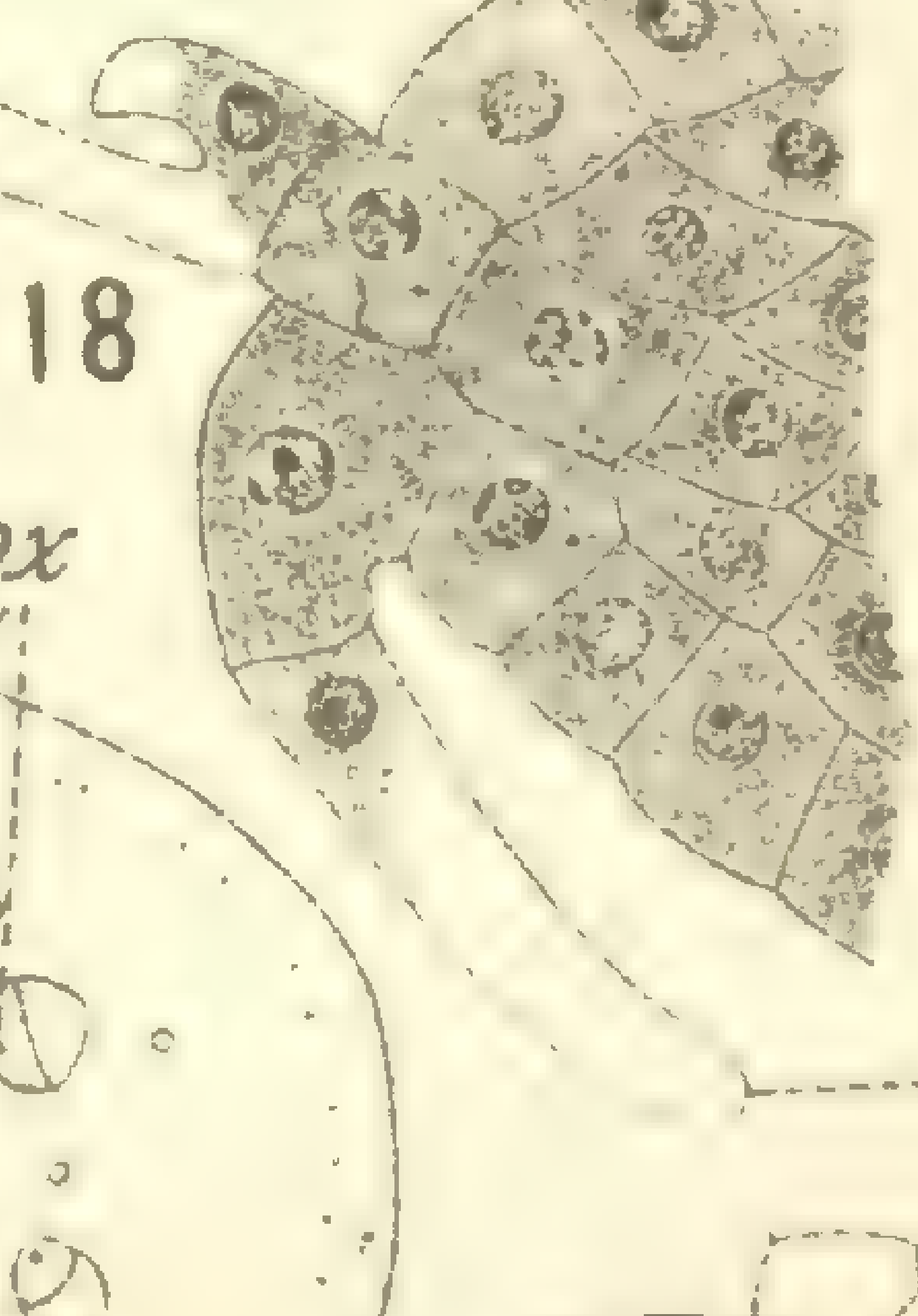

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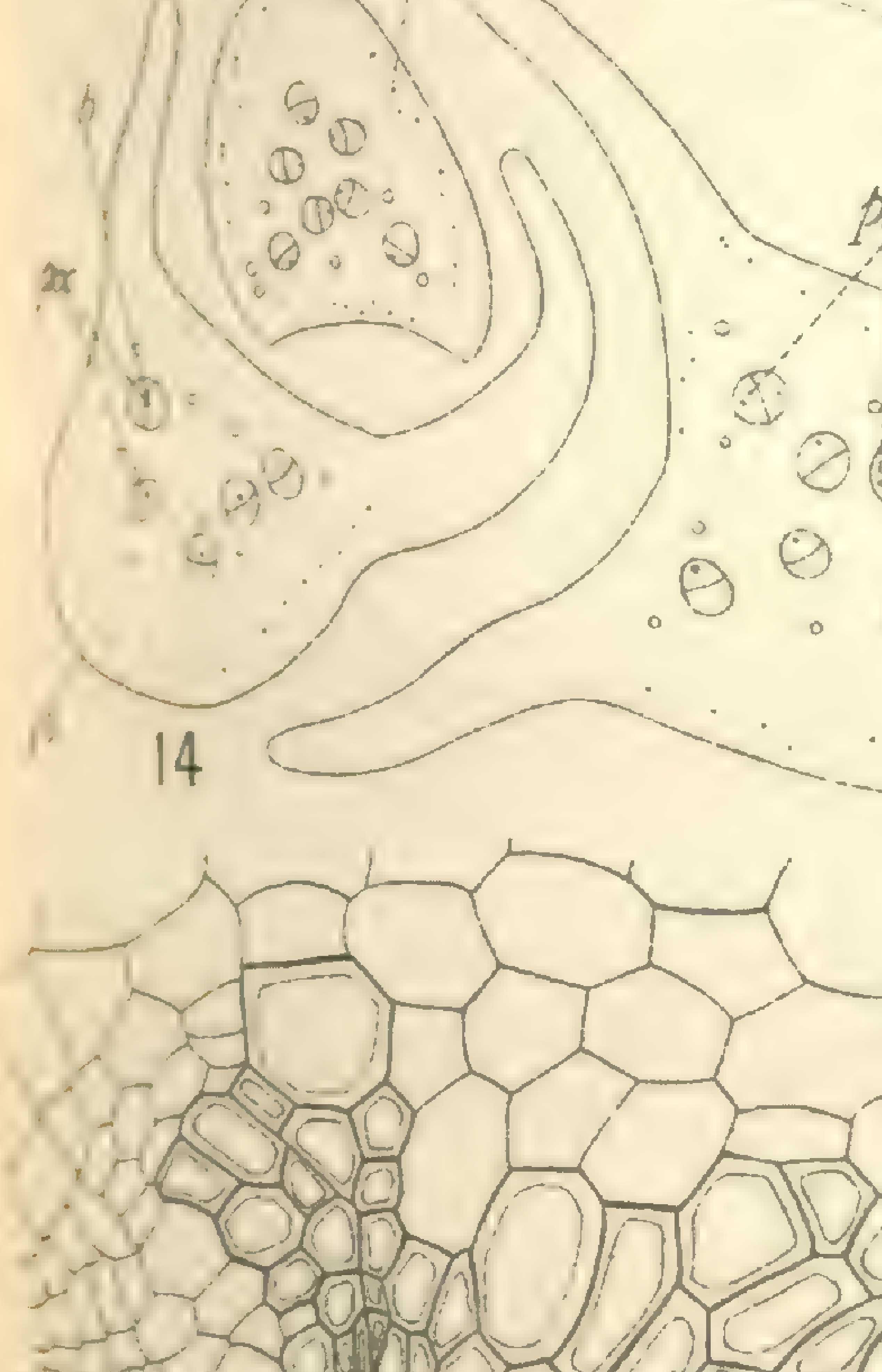

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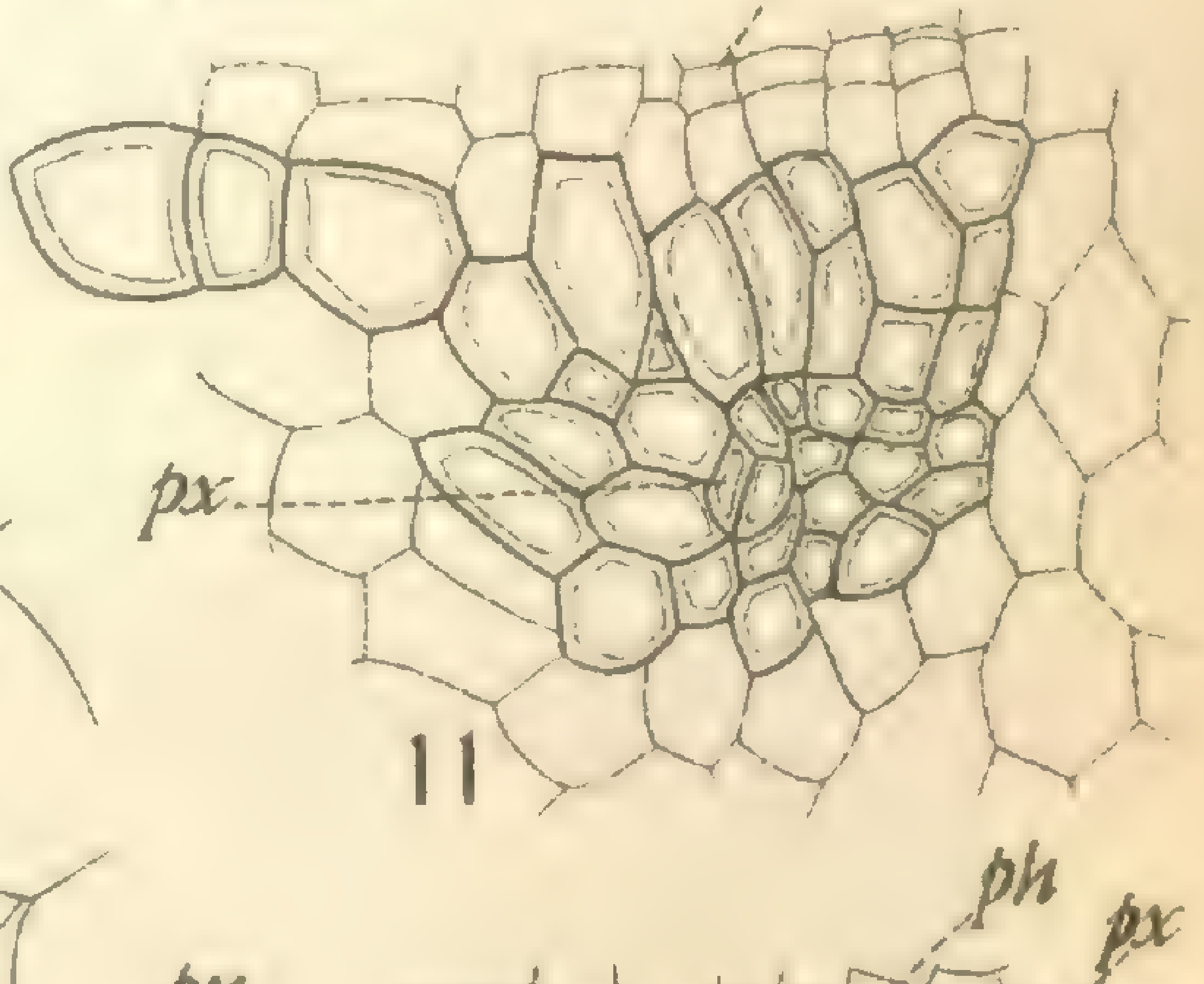

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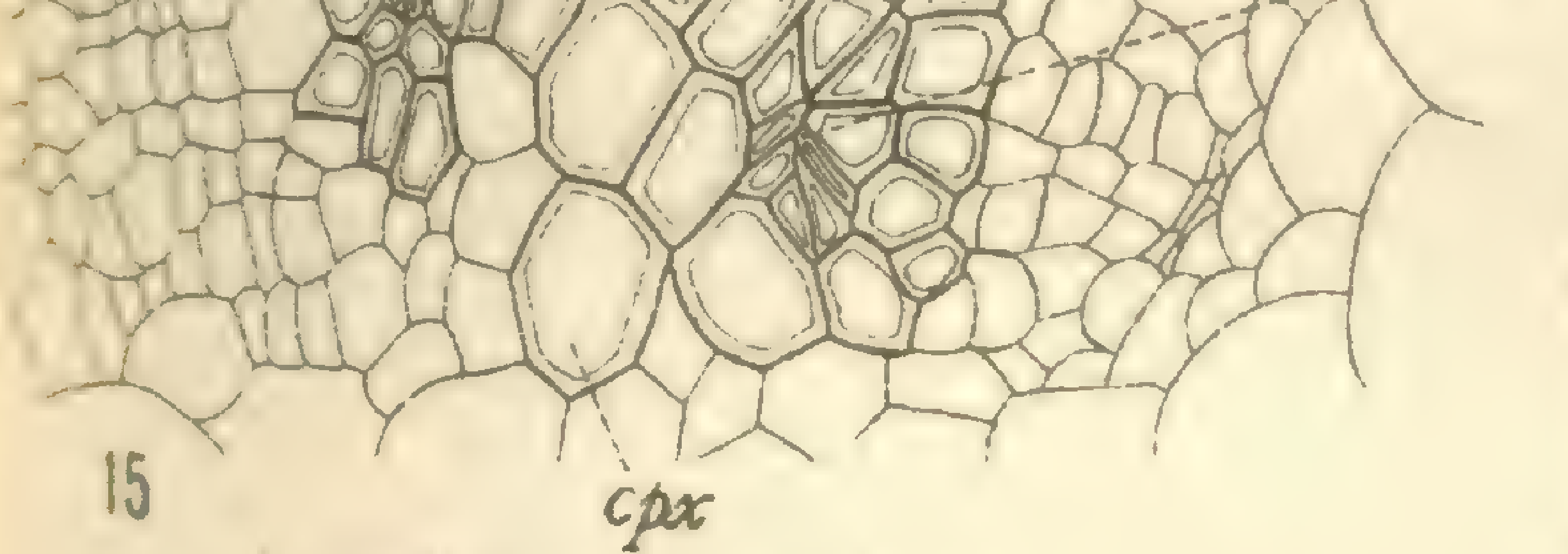

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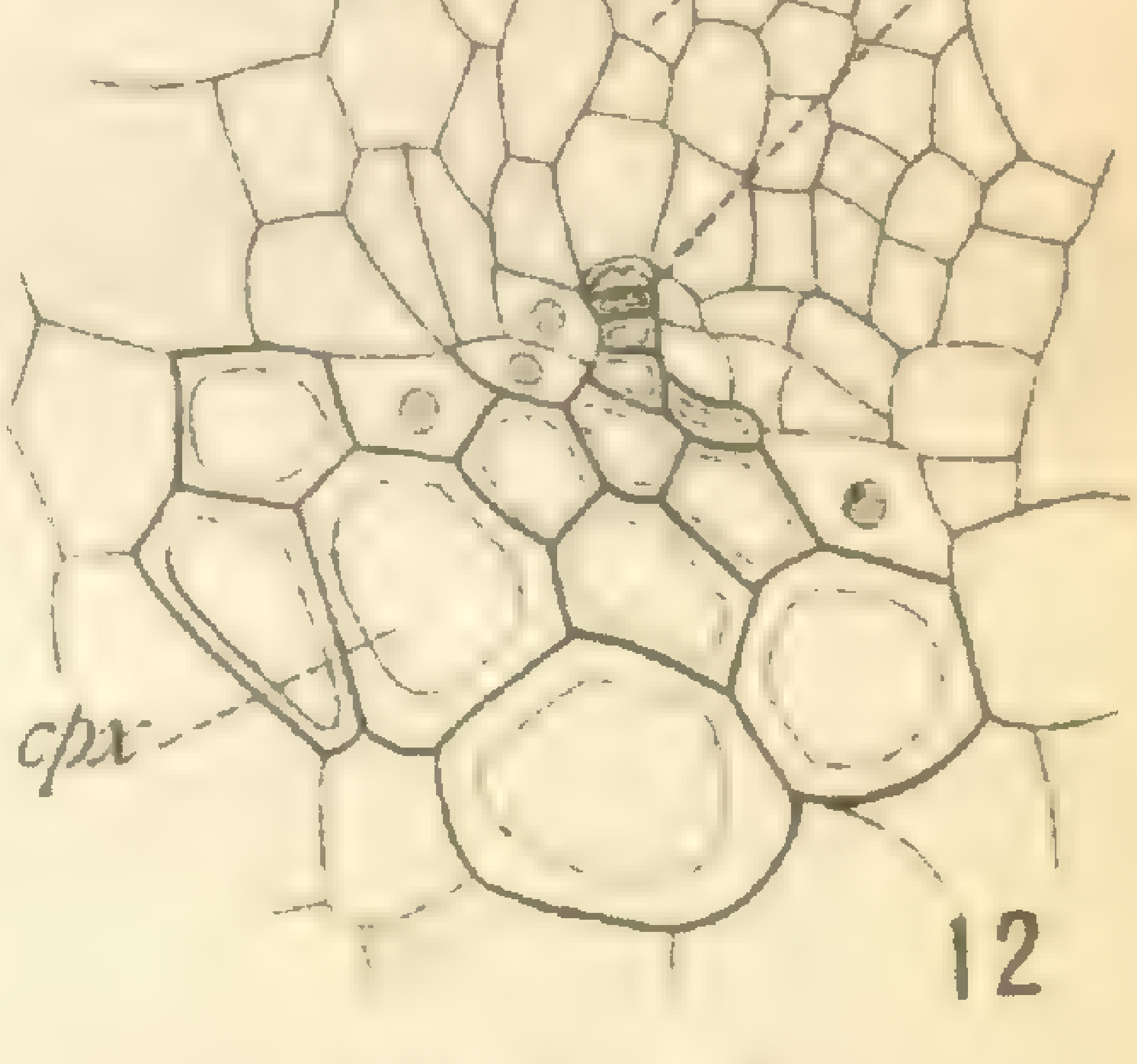

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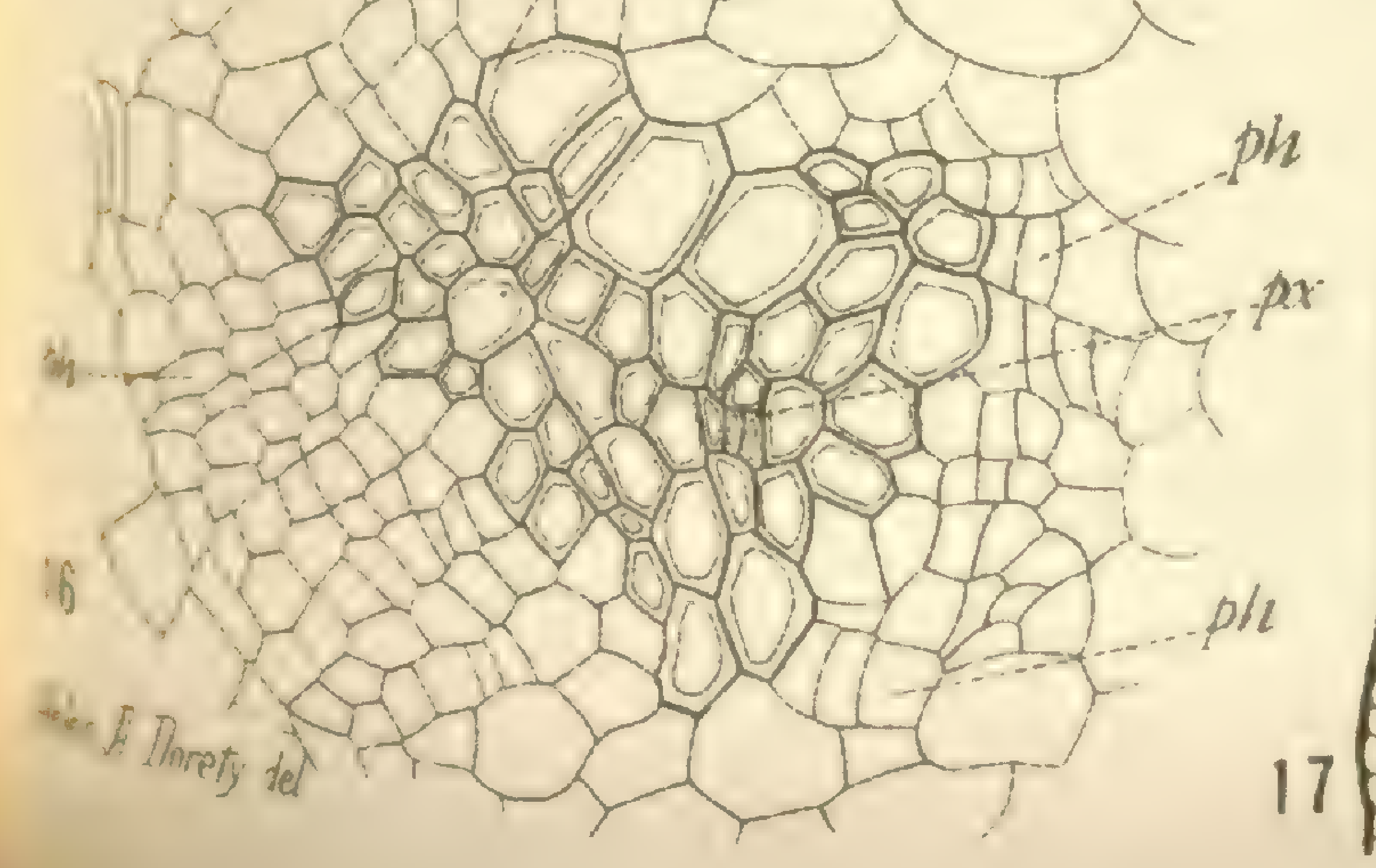
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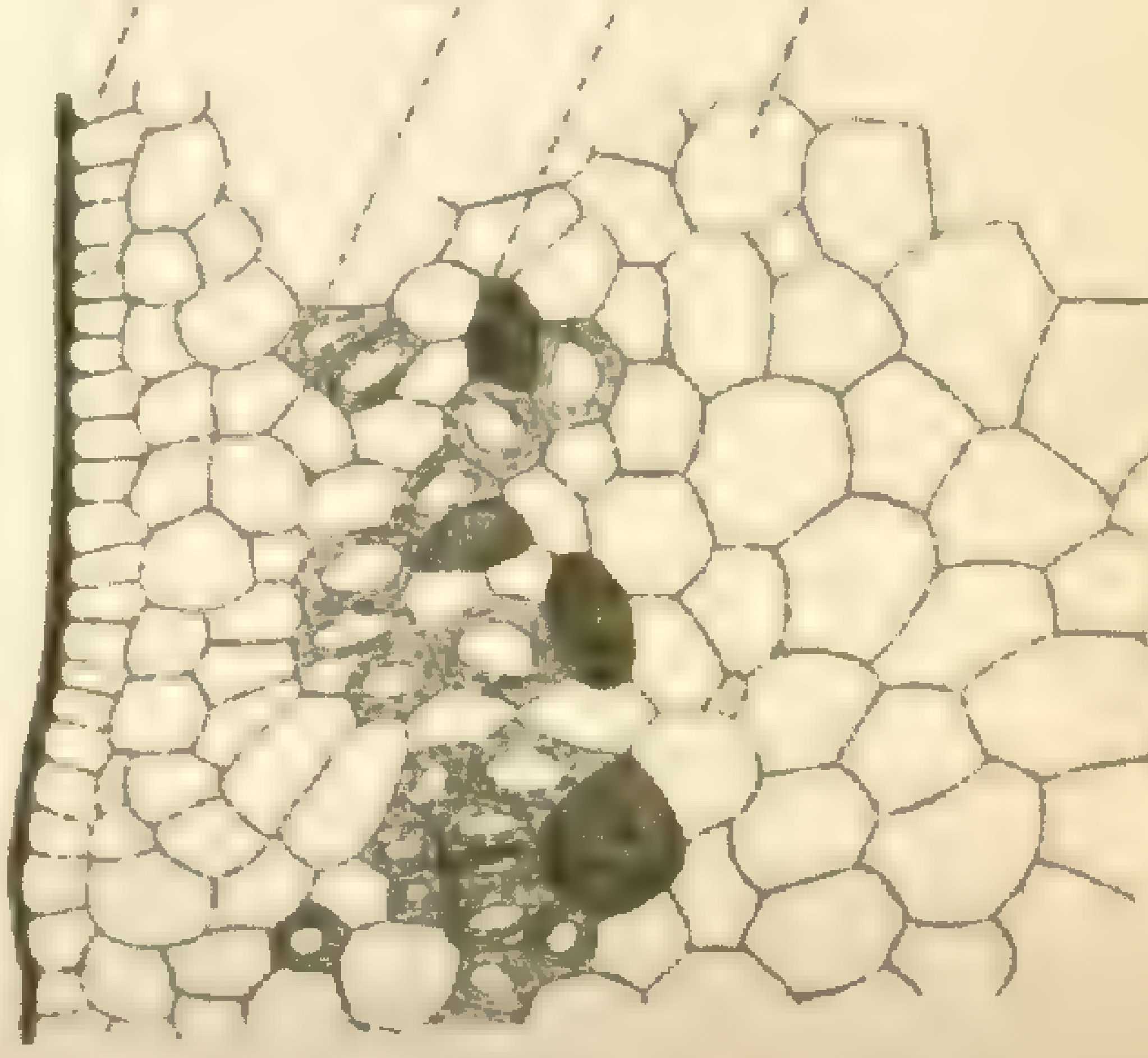

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FIG. 3a.—Detail from *fig. 3* showing one of the four cotyledonary traces near its point of insertion. ×60.

FIG. 4.—Base of the cotyledonary trace shown in *fig. 3a*. ×60.

FIG. 4a.—Diagram of stele of hypocotyl showing method of formation of root arrangement.

FIG. 5.—Exit of lateral root. ×60.

FIG. 6.—Diagram of root stele.

FIG. 6a.—Detail of one of the root poles. ×60.

FIG. 7.—Transverse section of the central vascular system above the cotyledonary node. It is composed of four groups of leaf traces. Semidiagrammatic.

FIG. 8.—Longitudinal section of portion of girdling leaf trace taken from transverse section of seedling. ×60.

PLATE VI

FIG. 9.—Transverse section of median traces of same leaf from same section as *fig. 8*. ×380.

FIG. 10.—Transverse section of leaf trace slightly above that represented in *fig. 9*. ×380.

FIG. 11.—Transverse section of same bundle 60 μ above section represented in *fig. 10*. ×380.

FIG. 12.—Exarch bundle from petiole 8^{mm} from base. ×380.

FIG. 13.—Transverse section of embryo, showing the sheath formed by the fusion of the cotyledonary petioles, the increase in the number of leaf traces in consecutive leaves, and their gradual assumption of the Ω arrangement. ×8.

FIG. 14.—Transverse section of three leaves in their natural arrangement, showing the relative amount of centrifugal wood at different levels of the petiole. ×8.

FIG. 15.—Approach of two leaf traces. ×380.

FIG. 16.—Fusion of some of the xylem elements of same to form a quasi-concentric strand. ×380.

FIG. 17.—Portion of peripheral region of tissue of petiole showing position of tannin cells. ×380.

FIG. 18.—Tip of young pinna showing unicellular hairs or ramentum. ×760.

BRIEFER ARTICLES

THE NATURE OF BALANCED SOLUTIONS

In his recent "Note on balanced solutions"[1] Professor Loew criticizes some of my statements. The following reply is inspired solely by the desire to obviate if possible any misunderstanding regarding the nature of a balanced solution.

A balanced solution is defined by Loeb as one in which the toxic effects which each salt would have, were it alone present in solution, are inhibited by one or more antagonistic salts in the solution.

Professor Loew objects to the term toxic as applied to calcium and potassium salts. His statement that I and a pupil claim to have discovered the poisonous action of potassium and calcium respectively is evidently due to a misapprehension. On the contrary, we treated them as fully accepted facts, and it was a surprise to us that he should call them in question. The poisonous action of a salt must be determined by comparing its effects with those of *pure* distilled water, or, in the case of strong solutions, with the effects of an isotonic balanced solution or an isotonic solution of an indifferent substance, if such can be found. In the absence of the facts needful for such a comparison, it is not possible to say whether the effects observed by him are to be regarded as toxic or not. At the concentration chiefly used in my experiments ($.12\,M$) roots of wheat reached a length in KCl of 63^{mm}, in $CaCl_2$ of 84^{mm}, in an isotonic balanced solution of 360^{mm}, and in distilled water of 740^{mm}. I may add that for certain forms of Vaucheria KCl and $CaCl_2$ at the dilution of $.001\,M$ (or even less) may be toxic, inasmuch as they kill the algae in three or four days, while in distilled water or dilute sea water of a hundred times greater osmotic pressure, they remain alive for many weeks. For such forms the components of Knop's solution including the K and Ca, taken individually, would prove poisonous. But for such plants as wheat the concentration of Ca and K used in Knop's solution is too weak to be regarded as toxic.

Professor Loew's designation of Knop's as a balanced solution seems, to say the least, very misleading. In a balanced solution the components are poisonous when taken separately. But Professor Loew tells us that neither calcium nor potassium salts are to be regarded as poisonous. They are important constituents of Knop's solution. How then does he regard it as a balanced solution? Only it would seem (since here the toxicity of the anions is negligible) by supposing that the sole poisonous constituent is magnesium, whose toxic action is completely inhibited by the calcium present. But on this view it is clear that the potassium and iron are completely superfluous from the standpoint of a balanced solution. Knop added them for nutrient, not for balancing, purposes, nor is there reason to suppose that he was aware of antagonistic salt effects. At the concentrations at which he worked these effects are not at all evident with such flowering plants as were used in his experiments. Under these circumstances the discovery of antagonistic salt effects is very improbable. For most of the plants for which Knop's solution is employed at its ordinary concentration, it is not a balanced solution, because its individual components are not sufficiently toxic to require balancing.

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[1] Bot. Gazette 46:302. 1908.

That to Professor LOEW is due the very great credit of investigating the antagonistic action of magnesium and calcium, and of making clear its economic importance, is acknowledged by all. These and other investigations made by him in the difficult and obscure field of the function of the mineral salts are of the highest value. Together with the experiments of other investigators they have thrown much light on antagonistic action. Inasmuch, however, as Professor LOEW apparently does not believe in generalizing the principle of antagonistic action, as Professor LOEB has done in his theory of balanced solutions, but prefers to restrict it to the single case of Mg *vs.* Ca, I find myself quite unable to agree with him. In the course of a series of experiments on wheat I have found antagonism between each of the following pairs of salts:

NH_4 *vs.* Ca
K *vs.* Ca
Na *vs.* Ca
Mg *vs.* Ca
NH_4 *vs.* Na
NH_4 *vs.* K
Na *vs.* K
Mg *vs.* K
Na *vs.* Ba
K *vs.* Ba
Na *vs.* Sr
K *vs.* Sr
Mg *vs.* Sr

One who has to deal with such a series of facts can hardly be expected to adopt a view which accounts for only one of these cases and ignores the rest, or explains them as due to the formation of double salts, particularly as such an explanation is wholly untenable in view of the facts of dissociation.—W. J. V. OSTERHOUT, *University of California, Berkeley.*

THE EXTRAFASCICULAR CAMBIUM OF CERATOZAMIA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 123

(WITH PLATE VII)

The anatomical features presented by the seedling of Ceratozamia described in a previous paper (3) gave promise of such phylogenetic importance that the study has been continued upon older stems. The interest centers mainly in the extrafascicular cambium—its origin, its distribution, and its failure to differentiate xylem and phloem which could be clearly recognized as such. In a careful examination of microtome sections of over eighty seedlings, varying in age from a few months to two years, only one small extrafascicular bundle was found.

The origin of the concentric vascular zones of cycad stems puzzled the early anatomists. BRONGNIART (1), failing to distinguish the phloem in these zones, regarded them as the equivalent of the seasonal wood rings of dicotyledons. VON MOHL (8) said that they were an aggregation of bundles which passed out from the central cylinder and, running downward in the cortex, grouped themselves in a ring. LESTIBONDOIS (4) saw individual bundles in the cortex, but thought they foreshadowed the breaking-up of the central stele, and so considered the cycads as a transition group from dicotyledons to monocotyledons. METTENIUS, to whom we are indebted for much of our knowledge of cycad anatomy, made no attempt to explain the extra vascular zones. CONSTANTIN and MOROT (2) thought that the tissue arose from the pericycle.

All the early research was confined to mature stems of Cycas and Encephalartos. In 1890, SOLMS-LAUBACH (7) reported the absence of such zones in *Ceratozamia mexicana*. In 1896 WORSDELL (9) added Macrozamia to the list of cycads in which these thickenings occur, and in 1898 (10) recorded their absence from the stem of Stangeria; in 1900 (11) he found them in the root of *Bowenia spectabilis*. His study of seedlings of species of Cycas (10) demonstrated to WORSDELL that the extrafascicular zones in mature stems arose as independent cortical cylinders arranged in distinct series, the innermost ones being composed of primary tissue. By a later growth of the central cylinder they become appressed to its periphery and flattened radially. This study brought to him and to his readers a conviction of the truth contained in his earlier suggestion that the cycads are closely related to the Medullosae, which are polystelic like the ferns. MATTE's study of *Cycas siamensis* and *Encephalartos Barteri* (5) is an almost perfect demonstration of WORSDELL's theory.

My work upon Ceratozamia will come as cumulative evidence. SOLMS's statement concerning the absence of extrafascicular zones is correct as far as the seedling is concerned; but the presence of extrafascicular cambium in great abundance led me to make a careful search to discover its relation to the central cylinder. In the study of seedlings described in the previous paper I was unable to do this on account of the disturbances caused by mucilage ducts, which are large, abundant, and irregular in distribution. In the study of older stems I have been more fortunate. Four-year-old seedlings have in the hypocotyl clearly distinguishable rings or cylinders of cambium. The cylinders are arranged in several series. Those of the innermost series, though decidedly flattened, are the most distinct.

Fig. 1 represents diagrammatically a section of the hypocotyl slightly below the exit of the cotyledonary traces. The innermost cylinders (*a*, *b*, *s*) arise in the pericycle near the transition region and are of primary origin. They extend well up in the stem, though pushed outward by the horizontal cotyledonary traces. The other rings appear later. It would seem that the single bundle described in the previous paper (**3**, *fig. 30*, *z*) was differentiated from one of the outermost series of cylinders.

Fig. 2 is a detail of the inner portion of half the section represented in *fig. 1*. One large cambial ring (*a*) is represented, and ends of two others (*b* and *s*). Several small rings (*e*, *r*) suggest how concentric bundles might arise.

The cause of the flattening is manifestly the enlargement of the central cylinder and the consequent pressure upon the inner side of the cortical cylinders (*a*, *b*, *s*). The final result is a central cylinder surrounded by several more or less imperfect zones of cambium cells. The xylem and phloem which these cells might produce would be oriented differently; the xylem on the centripetal side of the zone would be differentiated toward the periphery and the phloem toward the center of the stem. But in many cases, the inner cambium of each zone would cease to function, and we should then have successive zones of alternating xylem and phloem all with normal orientation. Occasionally a bit of the elongated cylinder would be disconnected, the cambium would round out, the growth of xylem would eliminate the pith, and a concentric bundle would result. All these conditions are found in the Medullosae, from the distinct fern-like polystely in *Medullosa Solmsii* and *M. anglica* to the condition of *M. stellata*, which closely resembles *Cycas revoluta*.

I have not yet examined mature stems of plants of this genus. WORSDELL (**9**) has confirmed SOLMS-LAUBACH's statement that the extrafascicular zones are lacking; but MATTE (6) reports that he saw them in stems which he examined. I am therefore in doubt whether it is an absolute failure to function, or only a delay; in either case we have an indication that the cortical vascular tissue is a disappearing character.

Another feature to which attention should be called is the constant occurrence of centripetal xylem in the cylinder of the hypocotyl and in the bases of the cotyledonary bundles. This is represented in *fig. 28* of the paper already cited and also in *fig. 2* of the present one. It is often relatively more abundant than in some stems of Lyginodendron. The stem cylinder above the cotyledons is endarch, the leaf traces becoming mesarch almost immediately after leaving the cylinder.

Acknowledgments are due to Professor JOHN M. COULTER and Dr. W. J. G. LAND.—HELEN A. DORETY, *The University of Chicago.*

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DORETY on CERATOZAMIA

CURRENT LITERATURE

BOOK REVIEWS

Gray's new manual of botany

It has been generally known for some time that GRAY'S *Manual* was undergoing a revision, so that the appearance of the seventh edition[1] was no surprise; in fact no book has been awaited by the botanical public, especially during the past three years, with so much interest as this one.

The present edition, contrasted with the sixth edition, presents the following more conspicuous changes: (1) a change in the geographical limits, namely by excluding the region west of the 96th meridian instead of the 100th, and in extending northeastward to include the maritime provinces and a portion of Quebec and Ontario; (2) the sequence of the families, which for the most part is in accordance with the system of EICHLER as elaborated by ENGLER and PRANTL; (3) the removal of the keys leading to the species, in the case of most of the larger genera, from the body of the text to a position immediately preceding the specific descriptions; (4) the introduction of numerous text- or marginal figures; and finally (5) in the use of a different system of nomenclature, namely the strict observance of the Vienna Code, or the nomenclatorial rules adopted at the International Congress held at Vienna in 1905.

The results of these innovations are that the flora treated is a somewhat more homogeneous one, the general arrangement and sequence of families is in accordance with advances made during recent years in the classification of plants, a greater facility and certainty in the identification of species by the use of direct keys and descriptions associated with accurately executed and reliable figures, and a greater consistency and uniformity in the use of plant names.

The general appearance of the printed page is essentially the same as in the sixth and in previous editions; the use of italics in emphasizing the more important specific characteristics is also retained. The treatment of genera and species is on the whole conservative and rational; and generic limitations are in close accord with general usage. The number of species is considerably larger than in previous editions, owing to the very active, careful, and exhaustive study of our flora during recent years.

The illustrations are judiciously distributed throughout the volume in groups where they are most useful, as, for example, in the Gramineae, Cyperaceae, Salicaceae, and Cruciferae; the Cyperaceae especially lend themselves to this type of illustration, and here they are certainly at their best. In some cases, for example in the Compositae, the illustrations have apparently suffered somewhat in the process of reproduction; thus for instance in the genus Crepis the illustrations, as reproduced, add little or nothing to the text. In general, however, the illustrations are excellent, and one only regrets that they are not more numerous.

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[1] ROBINSON, B. L., AND FERNALD, M. L., Gray's new manual of botany: a handbook of the flowering plants and ferns of the central and northeastern United States and adjacent Canada. Seventh edition, illustrated, rearranged, and extensively revised. 8vo. pp. 926. *figs. 1036.* New York: American Book Co. 1908. $2.50.

The presswork is exceptionally good; there are few typographical errors. On page 500, however, "Abizzia" occurs instead of Albizzia, which is evidently a misprint.

The value of this work as a textbook should not be overlooked. The discriminating text and complementary illustrations present the subject-matter in a satisfactory way for teaching purposes. The illustrations themselves are for the most part insufficient for the hasty determination of the species by the student, and they can be used to advantage only in connection with the brief but clear descriptions. In this regard the book has no equal.

On the whole this new edition of the well-known GRAY'S *Manual* presents a flora of the central and northwestern United States, and adjacent Canada in a single volume of convenient size and moderate price, thoroughly revised to date, incorporating the verified results of recent years of research, and fully accords with the most advanced and universally accepted views of taxonomy.—J. M. GREENMAN.

Heredity

A recent volume on heredity, by PROFESSOR J. ARTHUR THOMSON[2] of the University of Aberdeen, "is intended," as the preface states, "as an introduction to the study of heredity." The writer has long been known as the joint author with GEDDES of the *Evolution of sex*, but is perhaps most widely recognized as the translator of WEISMANN'S works and the exponent of Weismannism. A review of such a book in a botanical journal needs no apology, for much of the more recent work in heredity has been done with plants, and moreover the book deals with those general fields of biological research which must always be of equal interest to botanists and zoologists. These fields will ever be the meeting-ground of botany and zoology, because in this class of problems the organism is treated as such, and the fact that it is a plant or an animal is of minor importance.

The work is divided into fourteen chapters, and among the topics dealt with may be mentioned the physical basis of inheritance; heredity and variation; reversion; telegony; transmission of acquired characters; statistical and experimental study of inheritance; theories of heredity and inheritance; heredity and sex; and a final chapter is devoted to the social aspects of biological results.

Heredity and inheritance are defined as follows (p. 13): "By 'heredity' we do not mean the general fact of observation that like tends to beget like, nor a power making for continuity or persistence of characters—to be opposed to the power of varying—nor anything but *the organic or genetic relation between succes-*

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[2] THOMSON, J. ARTHUR, Heredity. pp. xvi+605. *figs. 49.* New York: G. P. Putnam's Sons. London: John Murray. 1908.

sive generations; and by 'inheritance' we mean 'organic inheritance'—all that the organism is or has to start with in virtue of its hereditary relation to parents and ancestors."

In the chapter on the physical basis of inheritance the author discusses the phenomena and experiments connected with chromosome reduction and fertilization, and concludes from the evidence that the chromosomes are the bearers of hereditary characters, but that "we should be chary in committing ourselves unreservedly to the conclusion that the heritable organization is *exclusively* resident in the chromatin of the nuclei of the germ cells." The chapter on heredity and variation contains a clear exposition of the facts and theories of mutation and continuous variation. The author believes that both are important evolutionary factors; that mutation, so far as present evidence goes, may have been a much more important factor in plants than with animals; and that the distinction between "large fluctuations" and "small mutations" is merely a verbal one. Regarding the causes of variation he considers it "useful to say that variation is the expression of a qualitative asymmetry beginning in gametogenesis." "Variation is a novel cell division."

There is a lengthy treatment of the question of the transmission of acquired characters or "somatic modifications;" with a critical analysis of the data usually cited as evidence. The result may be stated in the author's own words (p. 242): "The question resolves itself into a matter of fact. Have we any concrete evidence to warrant us believing that definite modifications are ever, as such or in any representative degree, transmitted? It appears to us that we have not. But to say dogmatically that such transmission is impossible is unscientific." The statistical studies of GALTON, PEARSON, and others are summarized, and under the experimental study of inheritance an array of data from the work of MENDEL, DEVRIES, BATESON, CORRENS, and many others of the recent school of genetics, which has begun to illuminate some of the obscure problems of hybridity, is brought together and discussed. These are largely the facts of Mendelism. In another part of the book blended, preponderant, and particulate inheritance are presented.

Other chapters are devoted to theories of heredity, which are largely theories of representative particles in some guise or other; and to theories of development, in which the author champions the determinants of WEISMANN and the latter's well-known theory of germinal selection. Under the topic heredity and sex, various theories of sex determination are discussed, including external and internal factors, and the author's theory is presented, namely that the difference in the sexes is merely a slight difference in "protoplasmic gearing" or in the "equation of metabolism." This view appears too vague to be of any value in directing the much-needed experiments on the subject. The author also apparently attaches too little significance to the discovery that in many insects an extra chromosome accompanies the female sex.

At the close of the work there is a representative bibliography of 48 pages, a very useful subject-index to the bibliography, and a general index to the volume.

The book is a broad and comprehensive treatment of the subject of heredity, a veritable mine of valuable data concisely presented and clearly discussed. The worker in these fields will find it almost indispensable for reference, and the more general reader will find it a very satisfactory and fascinating exposition of present-day views on these problems.—R. R. GATES.

Laboulbeniales

In 1896 the first part of a monograph of this group was published by THAXTER. The review in this journal[3] gave a general account of its contents, which presented the history, literature, and morphology of the group, in addition to the description of genera and species known at that time. During the last decade material has accumulated rapidly, and several preliminary papers describing it have been published. There has now appeared a second part of the monograph,[4] which brings together the material and illustrates it by a series of handsome plates. By means of visits to European collections and to South America, and through numerous correspondents, the new forms have multiplied remarkably. In the present part nearly 350 forms are illustrated, which increases the number described to about 500, included in more than 50 genera. In addition to these, more than 100 new species have been assembled since the completion of the present plates (in 1905), and these will be described and illustrated as soon as possible.

A brief review of the literature since 1895 is given, with comments on the morphology, development, etc., of the group, based upon the new data available. There is some modification in the conceptions of generic types, in the distinctions between series, etc.; but the comparative morphology of the group remains essentially as it was presented in 1895. This will be somewhat disappointing to those students of morphology who wish to relate Laboulbeniales positively to the Florideae; but the author wisely remarks that "it is foolish, on the basis of our present knowledge, to attempt an arbitrary settlement of the complex phenomena of series among the fungi." If he declines to be arbitrary about Laboulbeniales, no one else can afford to be so. Nevertheless, he thinks the statement safe that the group resembles the Florideae "in some respects more closely than they do any other plants, while at the same time they are more surely ascomycetes than many forms included in this group." He sees no reason why they should not be placed in the Pyrenomycetes, as a group coordinate with the Perisporiales, Hypocreales, etc.

This contribution, as the former one, is a model of painstaking and exact work, and of carefully weighed statement; and it is also an illustration of the wealth of material available for those who can see.—J. M. C.

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[3] BOT. GAZETTE 23:216. 1897.

[4] THAXTER, ROLAND, Contribution toward a monograph of the Laboulbeniaceae. Part II. Mem. Amer. Acad. Sci. 13:219–469. *pls. 28–61.* 1908.

African plants

Under the title *Die Blütenpflanzen Afrikas*,[5] Dr. Franz Thonner, after listing the chief botanical works and directing attention to some of the more scattered literature pertaining to the flora of Africa and supplying a detailed table of contents, gives a convenient key to the determination of the families of African flowering plants; then he presents the main body of the work, namely a key for the determination of the genera, which occupies about 540 pages. The text is supplemented by 150 plates, and a map indicating the floral regions and provinces of the continent.

Each family is described as to the essential and most striking characters and is represented, moreover, by a full page illustration of a characteristic genus; the number of genera and species of each family, so far as it occurs in Africa, is mentioned. Furthermore, the number of species in each genus and their geographical distribution is indicated.

The author presents no bibliography in connection with the text, and there is comparatively little in the way of synonomy; it is, however, definitely stated in the introduction that the limitations of families and genera are in accordance with Engler and Prantl's *Die natürlichen Pflanzenfamilien* and Dalla Torre and Harms's *Genera Siphonogamarum*, so that for critical identification it will be necessary to use the book largely in connection with these and other important works of reference.

The keys are ingeniously arranged, well contrasted, and lucid; the illustrations are clear and advantageously portray the general and detailed characters of the plant, and well represent the different families. The volume also contains a carefully prepared comparative table giving the number of families, genera, and species as well as their general geographical distribution; it also contains a glossary, a list of botanical authors, and a useful catalogue of the common African plant-names associated with the proper scientific name.

On the whole the work brings together in an epitomized form and in a single volume much information concerning the flora of Africa that hitherto has been scattered through many different volumes; hence it is a work which will be of great practical use both in the herbarium and in the field.—J. M. Greenman.

MINOR NOTICES

Das Pflanzenreich.[6]—Part 36 consists of a monographic treatment of the Nepenthaceae by the well-known writer and authority on insectivorous plants, Professor J. M. Macfarlane. An excellent general account of the family, following the usual sequence of this series, precedes the taxonomic consideration of the group. A concise dichotomous key leads one direct to the species under which are numerous references to literature, synonomy, a detailed description, concise statement of geographical range, and a rather full citation of exsiccatae. The author recognizes 58 species and several varieties for the one genus Nepenthes, of which 8 species and 4 varieties are here published for the first time. The main body of the work is followed by an alphabetical list of artificial hybrids. These are designated by the binomial under which is given, so far as known, the names of parent species. The family is illustrated by 19 figures; a complete index concludes the part. The production is quite in accord with previous publications of this comprehensive and admirable series, and it is pleasing to note the tendency toward international cooperation which is already manifest in the *Pflanzenreich*.

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[5] Thonner, Franz, Die Blütenpflanzen Afrikas: eine Anleitung zum Bestimmen der Gattungen der afrikanischen Siphonogamen. pp. xvi+673. *pls. 150. 1 map.* *M* 10 (12). Berlin: Friedländer & Sohn. 1908.

[6] Engler, A., Das Pflanzenreich. Heft 36 (iv. 111). Nepenthaceae von J. M. Macfarlane. pp. 92. *figs. 19 (95).* Leipzig: Wilhelm Engelmann. 1908. *M* 4.60.

Part 37, treating the Araceae[7] (begun in part 21 of this series), comprises: (1) a supplement to the Pothoideae in which a new genus (*Epipremnopsis*) is proposed with a single species, (2) an exhaustive treatise of the Monsteroideae, which reach their highest development in equatorial Asia and America, and in which group the authors recognize 12 genera and 190 species, 30 being new to science, and (3) an elaboration of the Calloideae with 4 monotypic genera. A concise key to the species precedes the larger genera, the species are clearly defined, and the numerous clean-cut illustrations happily combine general with essential detail characters.—J. M. Greenman.

Flora montana Formosae.[8]—This work concerns the mountain flora of the Island of Formosa, embracing the region lying at an elevation of 3000 to 13,000 feet. The total number of species recorded for this region is 392; the sebelong to 79 families and 266 genera. The author enumerates the various composing floral elements, such as the arctic, antarctic, alpine, tropical and North American, Malayan, Himalayan, southern, central, and northern Chinese, Japanese, and endemic. These upon summation show that "the flora is, in general, temperate, having as many as 320 species of temperate character, or 81 per cent. of the whole number of elements." The flora of the island has its strongest affinity with central and southern China and Japan, particularly as to the ratio of components, but as to their character "the flora of Formosa has as triking affinity to that of Japan." After a discussion of the general aspect of the vegetation and a division of the montane zone into four briefly characterized regions, the author follows with a detailed enumeration of the plants. In this list 69 species and 9 varieties are published as new to science. The descriptive matter is supplemented by several text-figures and carefully reproduced full-page illustrations. The work will serve as an excellent basis for future taxonomic investigation on the interesting flora of this island.—J. M. GREENMAN.

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[7] Engler, A., Das Pflanzenreich. Heft 37 (iv. 23 B). Additamentum ad Araceas-Pothoideas von A. Engler, Araceae-Monsteroideae von A. Engler und K. Krause, Araceae-Colloideae von K. Krause. pp. 1–160. *figs 60 (498)*. *M* 8.40. Leipzig: Wilhelm Englemann. 1908.

[8] Hayata, B., Flora montana Formosae. Jour. Sci. Coll. Tokyo **25**:1–260. *pls. 1–41*. 1908.

The United States as seen by de Vries.—Professor DE VRIES has published in the most attractive form an account of his experiences on his second American trip.[9] The volume is written in popular style, and is amply illustrated with unusually good half-tones depicting American scenery and universities. There are chapters on North Carolina with its cypress swamps and insectivorous plants; Arizona and the Grand Canyon; southern California with descriptions of San Diego, the marine vegetation of Santa Catalina, Pomona College, and a camping trip in the San Bernardino Mountains; the San Francisco earthquake, with special illustrations and descriptions of the disaster at Santa Rosa and Stanford University; the University of California, together with accounts of excursions to Mill Valley, Monterey, Mt. Hamilton, etc.; Great Salt Lake and Salt Lake City; agriculture in the central states, giving descriptions of the Kansas prairies, experiment stations and agricultural colleges in Kansas and Iowa, and maize culture in Illinois; and the dunes of Lake Michigan. One notices slight mistakes in the legends of two illustrations, a cut of Drosera being called Dionaea, and a scene among the University of Chicago buildings being attributed to the University of California. One in perusing this book longs for facility in the Dutch language, for the book contains the American impressions of one of the ablest men of our day. Botanists in these days too rarely write such volumes as this, perhaps because they feel that most of us are now globe-trotters, and able to be our own interpreters.—H. C. COWLES.

Algae and bryophytes of Connecticut.—The algae of the fresh waters of Connecticut have been described by Professor CONN and Mrs. WEBSTER in a preliminary report.[10] The descriptions and analytical keys and numerous drawings (from nature) bring these forms within easy reach of collectors and students.

The bryophytes of Connecticut have been described by Professor EVANS and Mr. NICHOLS.[11] An introduction (37 pp.) presents the general features of bryophytes, the history of their study in the state, their distribution according to environment, and their economic value. The catalogue, which includes keys and stations, makes the following enumeration: Marchantiales 12, Jungermanniales 92, Anthocerotales 3, Sphagnales 31, Andreaeales 2, Bryales 247, a total of 387. Of these, 68 are peculiar to America, 244 are common to Europe and Asia, 61 are common to Europe but not to Asia, and 14 are common to Asia but not to Europe. The bibliography of "Connecticut bryology" contains 81 titles.—J. M. C.

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[9] DE VRIES, HUGO, Naar Californië II. Haarlem: H. D. Tjeenk Willink & Zoon. 1907.

[10] CONN, H. W., AND WEBSTER, LUCIA W., A preliminary report on the algae of the fresh waters of Connecticut. pp. 78. *pls. 44* (*figs. 291*). Hartford: State Geol. and Nat. Hist. Survey, Bull. 10. 1908.

[11] EVANS, A. W., AND NICHOLS, G. E., The bryophytes of Connecticut. pp. 203. Hartford: State Geol. and Nat. Hist. Survey, Bull. 11. 1908.

British Basidiomycetes.—In 1905 the trustees of the British Museum secured the descriptions made by Mr. W. G. SMITH when preparing the series of colored drawings of British Fungi exhibited in the Department of Botany at South Kensington. Now these descriptions, accompanied by many line drawings illustrating generic characters, have been published as a handbook,[12] which it is hoped will be useful as an introduction to the field study of the fleshy fungi of Great Britain. A short introduction (8 pp.) gives a description of the general features and terminology of the group. The sequence followed is that of FRIES's *Hymenomycetes Europaei* (1874), which is followed also in Great Britain by BERKELEY, COOKE, and STEVENSON. Space has been saved by reducing the descriptions of species to the salient distinctive characters, which must be supplemented by the generic and sectional characters. The total number of species presented is about 2130, distributed among 128 genera and 11 families. The Hymenomycetes include about 2050 of the species, 106 of the genera, and 6 of the families. A full glossary and a complete index conclude the volume, which should certainly stimulate the interest and activity hoped for.—J. M. C.

Tabulae Botanicae.—This excellent series of botanical charts, published by Gebrüder Borntraeger (Berlin), has been appearing during the last two years, and has proved to be of unusual value. They are larger than the ordinary charts, so that they can be seen well in a large lecture-room. Even more important is the fact that they are not current illustrations selected by one person, but they are in a sense original productions, each chart being designed by a specialist in the group presented, and executed by an artist under his supervision. Thus BAUR has directed the illustrations of Myxobacteriaceae and Lichens, JAHN those of Myxomycetes, GUILLIERMOND those of the sexual forms of the yeasts, BLAKESLEE those of the mucors, etc. The charts have been raised slightly in price, being now *M*30 for a series of five unmounted. Dr. A. F. BLAKESLEE (Storrs, Conn.) has been asked to act as the American agent, and he will give information and transmit orders if desired.—J. M. C.

British Fungi.—In 1893 there was published a *Guide* to SOWERBY's models of British Fungi, exhibited in the Department of Botany of the British Museum (Natural History). The purpose of the models was to exhibit to the public such a series of edible and poisonous species as would help to prevent the fatal mistakes often made from eating poisonous species. The work of restoring the fragile models was committed to Mr. WORTHINGTON G. SMITH, and in connection with this the *Guide* was published. There has now appeared[13] a second edition which has been carefully revised, and a glossary has been added.—J. M. C.

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[12] SMITH, WORTHINGTON GEORGE, Synopsis of the British Basidiomycetes; a descriptive catalogue of the drawings and specimens in the Department of Botany, British Museum. 8vo. pp. 531. *pls.* 5. *figs.* 145. London: The Trustees of the British Museum. 1908. 10*s*.

Natürlichen Pflanzenfamilien.—Parts 231, 232, and 233 continue the presentation of mosses by V. F. BROTHERUS, completing Thuidieae, and presenting Hypnaceae, Leucomiaceae, Sematophyllaceae, Rhegmatodontaceae, and Brachytheciaceae.—J. M. C.

NOTES FOR STUDENTS

Current taxonomic literature.—A. D. E. ELMER (Leaflets of Philippine Botany 1:272–359. 1908) describes 100 new species of flowering plants, belonging to various genera, and (*idem* **2**:375–384) 9 new species of Lauraceae all indigenous to the Philippine Islands.—J. D. HOOKER (Hook. Ic. Pl. *pls. 2851–2875.* 1908) describes and illustrates 24 new species and one new variety of the genus Impatiens from China. The types are deposited either in the Paris, Le Mans, or Kew Herbarium.—V. L. KOMAROV (Acta Hort. Petrop. **29**:1–176. 1908), under the title of *Prolegomena ad floras Chinae nec non Mongoliae*, makes a valuable contribution to the literature concerning the flora of China; it includes, moreover, a critical revision of *Clematoclethra* Max., *Codonopsis* Wall., *Epimedium* and *Nitraria* L., in which genera 9 species and one variety are proposed as new to science.—HOMER D. HOUSE (Muhlenbergia **4**:49–56. 1908) gives a *Synopsis of the California species of Convolvulus.* The author recognizes 26 species, two of which are new.—W. P. HIERN (Journ. Bot. **46**:273–278. 1908) records the occurrence of a Sagittaria in the river Exe, near Exeter, England. The plant is described as a new variety of a North American species.—SPENCER LE M. MOORE (*idem* 290–298) describes 12 species of African plants as new to science, and proposes a new genus (*Grossweilera*) of Compositae; the same author (*idem* 305–313) characterizes 11 new species of African plants and a new genus (*Swynnertonia*) of the Asclepiadaceae, and also a new genus (*Eylesia*) of the Scrophulariaceae.—G. BONATI (Bull. Hb. Boiss. II. **8**:525–539. 1908) gives a synopsis of the genus Mazus. The author recognizes 24 species, 14 of which, and 2 varieties, are described as new.—J. BORNMÜLLER (*idem* 545–560) in a list of plants of the Elburz Mountains in northern Persia includes the description of a new species of Euphorbia.—FRANZ STEPHANI (*idem* 561–608, 661–696) describes 41 new species of Hepaticae, referred to various genera.—EDMOND MALINOWSKI (*idem* 623, 624) records a new species of Crucianella from Kurdistan.—HANS SCHINZ, in collaboration with different specialists (*idem* 625–640), describes 32 new species of African plants, including a new genus (*Pseudotragia*) of the Euphorbiaceae.—A. BRAND (Philip. Journ. Sci. **3**:1–10. 1908) gives a synopsis of the Symplocaceae of the Philippine Islands, in which 16 species are recognized, 6 of which, in addition to 3 varieties, are described as new.—T. NAKAI (Journ. Coll. Sci. Imp. Univ. Tokyo **23**:1–28. 1908) presents a careful synopsis of the Polygonaceae of Corea and describes one new species and a new variety in the genus Polygonum.—N. L. BRITTON (Bull. Torr. Bot. Club **35**:337–345. 1908), under the title of *Studies of West Indian plants, I*, describes 5 species as new to science.—IG. URBAN, in collaboration with different specialists (Engl. Bot. Jahrb. **42**:49–176. 1908), under the title *Plantae novae andinae imprimis Weberbauerianae, IV*, has published 173 new species and 25 new varieties of South American plants, and also 4 new genera: *Fiebrigiella* (Leguminosae), *Centradeniastrum* (Melastomaceae), *Guraniopsis* (Cucurbitaceae), and *Huthia* (Polemoniaceae).—HENRI LECOMTE (Jour. Botanique II. **21**:101–109. 1908) describes 7 new species of Eriocaulon from Indo-China.—ALFRED CHABERT (Bull. Soc. Bot. France IV. **8**:305–310. *pls. 12, 13*. 1908) proposes 2 new varieties of *Campanula rhomboidalis* L. from France.—G. BONATI (*idem* 310–314) describes 4 new species of Pedicularis from China.—F. GAGNEPAIN (*idem* 322–325) describes 2 new species of the Capparidaceae from China.—E. A. FINET (*idem* 333–343) has published 11 new species and 1 variety of orchidaceous plants from South America and from different parts of the Old World.—H. LÉVEILLÉ (*idem* 407–409) recognizes 5 species of Mucuna indigenous to China, 2 of which are described as new.—S. T. DUNN (Jour. Linn. Soc. London **38**:350–373. 1908) gives an account of *A botanical expedition to Fokien, China*, followed by descriptions of 37 new species and 1 new variety.—T. F. CHIPP (*idem* 374–391) in *A revision of the genus Codonopsis* recognizes 22 species, 4 of which are new to science.—Various authors, under the title *Diagnoses Africanae, XXIV* (Kew Bull. pp. 286–300. 1908), have published 16 new species and 5 varieties of African plants, including a new genus (*Cotylonychia*) of the Sterculiaceae, and also a new genus (*Hemandradenia*) of the Connaraceae.—HENRY PITTIER (Contrib. U. S. Nat. Herb. **12**:159–169. 1908), following a general discussion of the genus *Sapium* and an analytical key to the Mexican and Central American species, describes and illustrates the 9 species recognized for this region; of these 6 are new to science, and 4 are published in joint authorship with the late Prof. KARL SCHUMANN.—ED. PALLA (Oesterr. Bot. Zeitschr. **58**:389–392. 1908) describes 3 new species of Cyperaceae from Mexico and Colombia.—CHARLES BROOKS (Bull. Torr. Bot. Club **35**:423–456. 1908) gives an account of *The fruit spot of apples* and records a new species of the genus Cylindrosporium.—P. A. RYDBERG (*idem* 457–465) recognizes 6 species of Philotria for this country, one being described as new.—EUGENE P. BICKNELL (*idem* 471–498), under the title *Ferns and flowering plants of Nantucket, III*, has published 2 new species and proposes 7 new combinations chiefly in the genus Carex.—FRANK D. KERN (*idem* 499–511) in *Studies in the genus Gymnosporangium* publishes 3 new species and makes 3 new combinations.—F. PETRAK (Fedde, Rep. Nov. Sp. **5**:329–333. 1908) describes 9 new hybrids and 1 new variety in the genus Cirsium from southern Europe.—E. HACKEL (*idem* 333–335) records a new species of Phalaris from Australia.—F. KRÄNZLEIN (*idem* 369, 370) has described a new species of Calceolaria from Bolivia.—E. ROSENSTOCK (*idem* 370–376) has published 6 new species and 5 varieties of ferns from New Guinea.—J. BORNMÜLLER (*idem* 376, 377) records a new species of Reaumuria from Persia.—D. GRIFFITHS (Rep. Mo. Bot. Gard. **19**:259–272. *pls. 21–28.* 1908), under the title *Illustrated studies in the genus Opuntia—I*, has described 15 new species of Opuntia from Mexico and the southwest.—W. GUGLER (Ann. Mus. Hung. **6**:15–297. *pl. 1.* 1908), under the title of *Die Centaureen des Ungarischen National-Museums*, records in detail the species and subordinate categories of the genus Centaurea represented in the Hungarian National Museum; the work is preliminary to a monograph of this genus.—F. STEPHANI (Bull. Herb. Boiss. II. **8**:837–866. 1908) has described 45 new species of Hepaticae, of which several are American.—B. DE LESDAIN (Bull. Soc. Bot. France IV. **8**:420–424. 1908), under *Notes lichénologiques*, describes 3 species and 2 varieties as new to science.—H. LÉVEILLÉ (*idem* 424–427) enumerates 11 species of the genus Pueraria for China, of which 5 are published in joint authorship with VAUT.—P. DOP (*idem* 427–430) describes 3 new species of the Malpighiaceae from Indo-China.—F. GAGNEPAIN (*idem* 430–436) proposes 3 new species of the Zingiberaceae from Oceania.—H. DE BOISSIEU (*idem* 467–470) has described 4 species and 3 varieties of Violaceae from the Orient.—L. A. DONDE (*idem* 470, 471) has published a new species of Carya from Mexico.—H. COSTE (*idem* 472–476) records 2 new hybrids in the genus Cistus from southern France.—A. W. EVANS (Rhodora **10**:185–193. 1908) publishes further notes concerning New England Hepaticae. The total number of species in this group thus far recorded for New England is 147.—A. DAVIDSON (Muhlenbergia **4**:65–68. 1908) lists a collection of plants made in the Tehachapi Mountains, California, and proposes a new species in the genus Fritillaria.—D. PRAIN (Bull. Kew 381–387. 1908) gives a short history of Butea, a brief revision of the genus, and records 1 new species.—N. E. BROWN and O. STAPF (*idem* 407–412) describe 10 new species of African plants.—R. A. ROLFE (*idem* 412–416), under the title of *New orchids: Decade 32*, has published 10 new species.—T. F. CHEESEMAN (*idem* 419–421) records a new species of the genus Bagnisia from New Zealand.—E. DE WILDEMAN (Pl. Fl. Congo **2**:167–268. 1908), in connection with certain economic studies, has published 7 new species and 2 new varieties of Apocynaceous plants of Africa, chiefly from the Congo region.—B. SCHROEDER (Ber. Deutsch. Bot. Gesells. **26a**:615–620. 1908) has published 2 new species of Bacillariaceae from plankton of the Adriatic Sea.—J. H. MAIDEN and E. BETCHE (Proc. Linn. Soc. N. S. W. **33**:304–319. 1908) have published 5 new species and 3 new varieties of Australian flowering plants.—G. E. MATTEI (Boll. R. Orto Bot. Giard. Col. Palermo **7**:85–112. 1908), under the title *Contribuzioni alla Flora della Somalia italiana*, has described 9 new species of flowering plants.—C. S. SARGENT (Ont. Nat. Sci. Bull. 11–98. 1908) has described 44 new species of Crataegus from Ontario: the same author (Rep. Mo. Bot. Gard. **19**:35–126. 1908) proposes 69 new species of Crataegus from Missouri, and in another place (Bull. N. Y. State Mus. 122:26–130. 1908) 83 from New York.—C. H. PECK (*idem* 5–25, 131–160) has published 8 new species of fungi from New York.—H. CHRIST (Philip. Journ. Sci. **3**:269–276. 1908) has published 12 new species and 2 new varieties of Philippine ferns.—E. B. COPELAND (*idem* 277–284) describes 8 new species and 3 new varieties of ferns from China; and the same author (*idem* 285–300) presents *A revision of the Philippine species of Athyrium* in which 46 species are recognized, 5 species and 1 variety being described as new to science. —E. D. MERRILL (*idem* 307–315), under the title of *Philippine Freycinetia*, records 24 species of this genus from the Philippine Islands, 8 being described as new; and the same author (*idem* 317–338) has published 6 new species of oaks and 6 new species and 1 new variety of the genus Radermachera from the Philippine Islands. —R. WAGNER (Oesterr. Bot. Zeits. **58**:435–439. 1908) has described a new species of Tropaeolum from Columbia.—F. SENNEN (Bull. Acad. Intern. Geogr. Bot. III. **17**:449–480. 1908), under the title of *Plantes d'Espagne*, has published in joint authorship with C. PAU 6 new species and several new varieties of flowering plants from Spain.—R. FRIES (K. Sv. Vet. Akad. Handl. **42**:1–67. *pls. 1–7.* 1908) has published 23 new species and 14 new varieties of Malvales, chiefly from South America; the same author (*idem* **43**:1–114. *pls. 1–10.* 1908) recognizes 37 species for the genus Wissadula, of which 11 species and 4 varieties are described as new, and a new genus (*Pseudoabutilon*) of the Malvaceae is proposed, to which are referred 9 species, 3 being new to science.—K. JOHANSSON (Arkiv för Botanik **7**:no. 12, pp. 48. *pls. 1–5.* 1908), under the title *Hieracia vulgata Fr. från Torne Lappmark*, enumerates 35 species, 20 of which and 3 varieties are described as new.—J. M. GREENMAN.

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[13] SMITH, WORTHINGTON GEORGE, Guide to SOWERBY'S models of British Fungi. Second edition, revised. pp. iv+85. *figs. 91.* London: The Trustees of the British Museum. 1908.

Effect of light on germination of seeds.—HEINRICHER[14] has recently added two more papers to his series on the effect of light on germination, and KINZEL[15] publishes a second paper (preliminary statement) on his extensive researches on this subject. Data enough are now at hand to get at some general principles. In respect to the effect of white light upon their germination, seeds may be divided into four groups: those requiring light for germination (*Rhododendron javanicum*, *R. hirsutum*, *R. ferrugineum*, *Drosera capensis*, etc.); those germinating more quickly and fully in light (*Veronica peregrina*, *Allium suaveolens*, etc.); those germinating equally well in light and darkness (*Myrmecodia echinata*, etc.); and those retarded in germination by light (*Phacelia tanacetifolia*, *Pedicularis Sceptrum Carolinium*). It is agreed by both authors that the favorable effect of light is not due to its causing an early carbon assimilation, but rather to its effect upon enzyme activity on production and therefore upon the digestion of stored foods. The conclusion concerning photosynthesis seems to be justified, for in all cases tested the light is as effective in CO_2-free chambers as in chambers containing CO_2. The effects of different rays as stated in the following paragraph also seem to support this conclusion. I see no grounds, however, for concluding that the effect is upon the digestive enzymes rather than upon some other mechanism of the protoplasm.

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[14] HEINRICHER, E., (1) Beeinflüssung der Samenkeimung durch das Licht. Wiesner-Festschrift. Wien. 1908. (2) Die Samenkeimung und das Licht. Ber. Deutsch. Bot. Gesells. **26a**:298–301. 1908.

[15] KINZEL, W., Die Wirkung des Lichtes auf die Keimung. Ber. Deutsch. Bot. Gesells. **26a**:105–115. *figs. 4.* 1908.

Kinzel's attention has been largely centered upon the effects of rays of different refrangibility. Heinricher[16] early found that the red end of the spectrum was most effective in *Veronica peregrina*. Kinzel's results indicate that this is generally the case. Among different species, however, there is a great variation in the relative effectiveness of various rays. Green is by far the most effective with Nicotiana, while with Veronica yellow gives the greatest stimulation. Kinzel finds the blue rays least effective; in fact they often cause marked retardation. In many cases of seeds favored in germination by light, blue gave a much slower and lower percentage of germination than darkness. Kinzel comments upon the general retarding effect of blue light, while Heinricher later points out that in the seeds of *Phacelia tanacetifolia* which are retarded in germination by white light, blue markedly stimulates germination.

Many of the "light-loving" seeds demand a considerable period of rest after harvest, during which they become thoroughly dried out. In *Veronica bellidioides* three and one-half months was the most effective period. In the short-lived seeds of Drosera fifteen hours of drying in the laboratory best effected their "after-ripening." Heinricher says, "On the whole the experiments indicate that the results in the germination of such seeds as are helped by light depends upon the age of the seed, upon the quickness of drying after harvest, further, also, upon whether this takes place in light or darkness, and, if in the first way, whether in one layer or several. Finally, even the moisture content of the air during storage must be considered as a factor. It is evident that the conditions are extraordinarily complex and that conformity of results is to be expected only under the consideration of all these factors."

Heinricher believes that the similarity in behavior of various seeds toward light is more often connected with their phyletic relationships than with likeness of ecological habit.

It seems to the reviewer that in cases where evident coats appear, the investigators should work with coat-free seeds to make sure that the coats by partial exclusion of oxygen, salts, or even water are not hindering germination. In such cases light may be a means of compensating some other limiting condition of germination. It is also evident, from the variable results, that the real solution of the problem will come from learning the particular dormant process in each case that is aroused by light. This ought to be possible in view of the great advance being made in our knowledge of the catalytic nature of protoplasmic activity, but it will demand an attack on the problem from other points than the mere effects of light upon the living seeds.—Wm. Crocker.

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[16] Heinricher, E., Ein Fall beschleunigendes Wirkung. Ber. Deutsch. Bot. Gesells. 17:308–311. 1899.

Observations on Welwitschia.—PEARSON has communicated further studies on this peculiar genus to the Royal Society, London, of which the following is an abstract.

Macrospores and embryo sacs are frequently present in the pith region of the female cone-axis. This confirms the view, already adopted by most authors, that the ovule of Welwitschia is cauline. Sporogenous cells have not been found in a similar position in the male cone.

It is suggested that the female cone and the male flower are derived by reduction and specialization from an amphisporangiate strobilus of a type similar to that of Bennettites.

At the end of the free nuclear division the embryo sac contains about 1024 nuclei which are equivalent in all visible characters. Cleavage of the cytoplasm occurs, resulting in the septation of the whole sac into compartments. Those near the micropylar end contain few nuclei which are functionally sexual; most of those of the lower three-fourths inclose many potentially sexual nuclei. The former send out embryo-sac tubes into the nucellar cone and into them pass the cytoplasm and free nuclei; all the nuclei in each of the latter fuse so that each compartment becomes a uninucleate cell. The compartments containing the fusion nuclei form the primary endosperm, whose later growth is distributed over two periods, one before and the second after fertilization. The endosperm of Gnetum is probably formed in the same way. In respect of the morphological character of the endosperm, Gnetum and Welwitschia are widely separated from Ephedra, in which the endosperm is a prothallus of the normal gymnosperm type. It is suggested that the endosperm of the primitive angiosperms was homologous with that of Welwitschia.

The embryo-sac tubes meet the pollen tubes in the lower half of the nucellar cone. Fertilization occurs within the generative cell, which enlarges after leaving the pollen grain and its nucleus divides. The daughter nuclei are functional gametes.

Several oospores are commonly formed in each nucellus. The cytoplasm of the oospore is mainly, if not entirely, provided by the generative cell. A resting nucleus is formed. The oospore elongates toward the top of the endosperm. The first nuclear division within it is followed by the formation of a centripetally developed wall which separates the upper "primary suspensor" from a lower terminal cell. From the latter are developed: (*a*) 24 cells which, surrounding the lower part of the primary suspensor, form with it "the secondary suspensor;" (*b*) a terminal group inclosing a presumed embryonic plate of eight cells. The later stages of embryo development have not been seen; they possibly occur, as in Gnetum, after the seed is detached from the plant.

It is suggested that (1) the Gnetum-Welwitschia alliance has its origin in the same stock as the angiosperms, but separated from the angiosperm line before the carpel became the pollen-receiver; (2) Welwitschia is the most specialized living representative of the race to which it belongs.

Mucilage ducts in Pipereae.—In considering the genera of the Piperaceae, two tribes are recognized by VAN TIEGHEM,[17] namely Pipereae and Peperomieae; while the Saururaceae are kept as a distinct family, as suggested a hundred years ago by L. CL. RICHARD. By CASIMIR DECANDOLLE the Saururaceae were replaced in Piperaceae as a tribe; and then separated by ENGLER. In speaking of Piperaceae, therefore, VAN TIEGHEM does not include Saururus and its allies. From an anatomical point of view the Piperaceae have long attracted much attention, especially on account of peculiarities in stem structure, which at the same time are characteristic of the respective tribes. For instance, in the Pipereae the stem exhibits a normal monostelic structure, with the broad stele surrounded by a well-differentiated endodermis, and possesses at least two concentric bands of mestome bundles. In the Peperomieae, on the other hand, the stem structure is of the schizostelic type, the numerous meristeles being scattered, not arranged in bands, and each being provided with a special endodermis. Common to both tribes, however, is the presence of roundish oil cells with the cell wall suberized or at times lignified; these oil cells are widely distributed through stem and leaf. In certain Pipereae still another secreting system occurs, which is now for the first time described. It consists of a single duct or several broad ducts containing mucilage and extending through the full length of stem and leaf; these ducts are lysigenous, since they arise from the destruction of a row of secreting cells. They occur in the pith of the stem, mostly a very broad one in the center and several narrower ones in a band around this and alternating with the innermost mestome strands. They contain a colorless mucilage, and are surrounded by small cells, notably smaller than those of the surrounding pith parenchyma. This system of secretory ducts belonging to the stem stele is readily followed through the internodes, but disappears completely in the nodes. In the leaf these ducts occur in the petiole, in the parenchyma located on the ventral (the hadromatic) face of the arch formed by the mestome strands; thence they may be traced in the midrib of the leaf blade, from the base to apex. Although the author examined various representatives of the Peperomieae, he failed to detect the ducts in any of them. Among the Pipereae they occur in Piper (as in *P. nigrum*, *P. Cubeba*, *P. macrophyllum*, etc.), in *Chavica Blumei*, *C. sphaerostachya*, and some species of Heckeria; while they are not developed in Macropiper, Nematanthera, and Zippelia.—THEO. HOLM.

Studies in aquatic plants.—FRANÇOIS[18] has offered a very interesting contribution to the knowledge of aquatic plants with notes on their structure, external as well as internal, and on their seedlings, the text containing many well-drawn figures. Special attention is given to the vegetative reproduction of such species as occur on river banks, the stolons of which grow in the water, creeping over the muddy bottom. Among these are *Mentha aquatica*, *Lysimachia vulgaris*, *Lycopus europaeus*, *Stachys palustris*, partly also *Potentilla reptans*, *Ranunculus repens*, and *Cynodon Dactylon*. In these the vegetative reproduction is amply secured by the ability of the fragments of the rhizomes and stolons to root very easily, and at the same time the water currents help to disperse such fragments over wide areas. The seedling stage of Butomus, various species of Alisma, Sagittaria, Najas, and Potamogeton is described. The slow growth of the primary root is characteristic, while the hypocotyl attains its final length in a very short time, and before the root actually commences its increase in length. The primary root stele in Butomus and in Alismaceae consists of a single central vessel and of two strands of leptome diametrically opposite each other. In the Najadaceae, on the other hand, several vessels are developed, the largest of which is usually located in or near the center, and there are also several strands of leptome, corresponding in number with the rays of hadrome. The hypocotyl exhibits a bilateral structure in Butomus and Alisma and no pericycle was observed inside the endodermis. In the Najadaceae the bilateral structure is much less pronounced, and no stomata were observed in the epidermis of the hypocotyl of any of these plants. A very simple structure characterizes the cotyledon; the chlorenchyma is homogeneous and contains only one vein near the ventral face. The seedling stages are very carefully described and figured, adding several interesting points to the knowledge of the structure of aquatic plants.—THEO. HOLM.

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[17] VAN TIEGHEM, PH., Sur les canaux à mucilage des Piperées. Ann. Sci. Nat. Bot. IX. 7:117. 1908.

[18] FRANÇOIS, L., Recherches sur les plantes aquatiques. Ann. Sci. Nat. Bot. IX. 7:25. 1908.

Organic correlations.—EAST[19] attempts a classification of correlations with especial consideration of plant data. This is a little-known field at the present time, but one of great promise for the future. The writer of course realizes that this tentative classification awaits the accumulation of further data to place it on any satisfactory basis. Correlations are considered as "somatic" and "gametic." Under somatic correlations are classed: (1) correlated reactions to environment; here are placed the experimental results of MACDOUGAL in Raimannia and of TOWER in Leptinotarsa, although the indications are that these changes are germinal and not somatic; (2) growth correlations between (*a*) non-homologous, (*b*) homologous, and (*c*) meristic parts; (3) correlations in organs of a plant; (4) interdependent and exclusive development; here is cited the case of *Oenothera lata*, in which the broad-leaved character is associated with the "inability to produce healthy pollen;" but this association is not constant, for plants from England having the *O. lata* characters have been successfully self-pollinated;[20]

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[19] EAST, EDWARD M., Organic correlations. Amer. Breeders' Assoc. **4**:pp. 12. 1908.

[20] MACDOUGAL, D. T., VAIL, A. M., AND SHULL, G. H., Mutations, variations, and relationships of the Oenotheras. Carnegie Inst. Publ. **81**:pp. 92. 1907; and unpublished results of the reviewer.

(5) heterozygotes; in the numerous cases where heterozygotes differ from either parent, "the ability to transmit certain characters is correlated with other *apparent* characters." Under gametic correlations are placed the phenomena of partial and complete "coupling," so called, developed chiefly by BATESON.—R. R. GATES.

Tyloses in ferns.—It has been noted by various writers that in the stems and petioles of ferns the protoxylem groups suffer disintegration, and into the cavities so formed the wood-parenchyma grows, forming the "cavity-parenchyma" of Russow. Proliferations from these cells frequently fill the cavities, and present the appearance of tyloses. These growths have recently been studied in detail by two independent workers, KIRSCH[21] and Miss MCNICHOL.[22] Both writers show that the phenomenon is widespread, being found in nearly every family of the true ferns, as well as in Marsilia and the Ophioglossaceae. In both papers the cells in question are carefully described and their origin as stated above is proven. KIRSCH has studied *Pteris aquilina* in most detail, and finds cavity-parenchyma in the stipe and in all regions of the rhizome, where it occurs in the outer system of bundles which he erroneously regards as cortical (p. 388). He offers the following as a theory of the cause of these growths: the cavity formed by disintegration of the protoxylem at first functions as a water duct; later the metaxylem (secondary xylem according to KIRSCH) makes its appearance and performs the duty of water carrier. Hence the pressure in the cavity is reduced, and as a consequence tyloses grow into it.—M. A. CHRYSLER.

Composition of a field of maize.—A brief paper by SHULL[23] calls attention to the view, already expressed by DEVRIES and others, that a field of corn, like wheat and other grains, is made up of a number of elementary species or biotypes. He discusses the fact that inbreeding in corn results in deterioration, and points out that the old hypothesis that the deleterious effects of inbreeding result from the accumulation of disadvantageous individual variations to form an organism with an inharmonious or unbalanced constitution, is untenable, in view of the facts of cleistogamy, self-pollination, and parthenogenesis in plants which have evidently been successful in the struggle for existence. A cornfield is conceived to be a series of hybrids between elementary species, and on the basis of the common observation that hybrids between nearly related forms are more vigorous than either parent, he believes that over-selection, which eliminates down to a single biotype, results in deterioration, not intrinsically from inbreeding, but because the greater vigor which comes from the crossing of biotypes has been eliminated. The ideal of the corn-breeder should then be continuous hybridization between biotypes, rather than the isolation of pure strains.—R. R. GATES.

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[21] KIRSCH, SIMON, On the development and function of certain structures in the stipe and rhizome of *Pteris aquilina* and other Pteridophytes. Trans. Royal Soc. Canada III. 14:353–412. *figs. 27+21.* 1907.

[22] MCNICHOL, M., On cavity parenchyma and tyloses in ferns. Annals of Botany **22**:401–413. *pl. 25.* 1908.

[23] SHULL, GEO. H., The composition of a field of maize. Amer. Breeders' Assoc. **4**:pp. 6. 1908.

Isolation and mutation.—While the final adjudication of the claims of the various theories of evolution must be made on an experimental basis, such data must be in harmony with the facts of plant and animal distribution, as is pointed out in a suggestive paper by LEAVITT.[24] It is of much interest to observe that zoologists, as a rule, have been less inclined to believe in mutation than have botanists. This is in part due, LEAVITT thinks, to a less perfect grasp of the theory by some of the zoologists, but in part due also to the fact that most students of animal distribution believe that isolation of closely related species is a most important principle in evolution. The author shows that there are innumerable cases of overlap in closely related plants of all groups, most notable, perhaps, in the widely varying thallophytes and bryophytes, but abundant in the seed plants. There is plenty of evidence that new species may have originated from the old without geographic isolation, although cases suggesting the latter are not wanting. Therefore, it is concluded, many facts of plant distribution favor the mutation theory, though they do not show that this is the only valid theory of evolution.—H. C. COWLES.

Osmotic properties of root hairs.—HILL[25] has investigated the osmotic properties of the root hairs of *Glyceria maritima*, *Suaeda maritima*, and *Salicornia herbacea*, which grow in a salt marsh subject to great changes in the osmotic pressure of its soil water, due to periodic flooding by the tides and to occasional drenching rains. He finds that the hairs show marked and rather rapid variation in osmotic pressure corresponding in variation to the osmotic pressure of the soil water. This variation is not due to the entrance of the abundant chlorids of the soil water, for in no case could he find chlorids in the root hairs, although they could be found in traces in the upper portions of the seedlings. The high osmotic pressure of the soil water seems to act through the irritability of the protoplasm, causing a dissociation of the compounds of the cells. He thinks OSTERHOUT is wrong in concluding that osmosis is not an important process in plant nutrition, and points out the fact that all the data of this investigator can be explained by the fact that plants can modify their osmotic properties readily in response to and in protection against rapidly varying external osmotic pressures.—WILLIAM CROCKER.

Statolith theory.—BUDER[26] comes to the support of the statolith theory with a set of well-chosen and critical experiments that seem to justify his conclusions, which are briefly as follows: Contrary to FITTING'S conclusion, in a combination of the rest position with various angles, the statolith starch takes the position that would be expected by the statolith theory. Centrifugal acceleration causes the movement of the starch that the hypothesis assumes, as shown by accelerations from 0.13 *g* to 9 *g*. In these various accelerations the time of the movement of the starch to the side of the cells coincides with the presentation time as determined by BACH. In the intermittent exposures of opposite sides when these exposures are of short duration the starch moves to the side of the cell of the most effective exposure only after the process is long continued, corresponding to the slow reaction in these cases. However well this paper may answer a number of the arguments against the statolith theory, there are yet a number unanswered and this whole matter of geotropic reaction seems too complex to be entirely explained in such a simple way.—WM. CROCKER.

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[24] LEAVITT, R. S., The geographic distribution of nearly related species. Amer. Nat. **41**:207–240. 1907.

[25] HILL, F. G., Observations on the osmotic properties of the root hairs of certain salt marsh plants. New Phytologist **7**:133–142. 1908.

[26] BUDER, JOHANNES, Untersuchungen zur Statolithenhypothese. Festschrift zur Feier des 25-jährigen Bestehens der Deutsch. Bot. Gesells. Ber. **26**:162–193. 1908.

Ray-tracheids in Cunninghamia.—The complex structure of the medullary rays of living Abietineae, consisting of parenchyma cells, ray-tracheids, and an elaborate system of ligneous resin-canals, has been used as one of the evidences of a highly specialized and relatively modern group. JEFFREY[27] has studied the marginal ray-tracheids that occur occasionally in Cunninghamia and has found them to be due to wounding, being most numerous in the region of the injured annual rings opposits the wound-callus. They resemble in general those described for certain genera of the Taxodineae and Cupressineae, and JEFFREY thinks that this is additional evidence that these two tribes have been derived from the Abietineae, the ray-tracheids being "vestigial or reversionary." He emphasizes this view by calling attention to the fact that there is no evidence that the Taxodineae and Cupressineae existed before the end of the Cretaceous. Such conclusions illustrate the fact that apparent simplicity of structure may not indicate greater antiquity than greater complexity of structure.—J. M. C.

Vascular system of Ranales.—WORSDELL[28] maintains that the primitive angiosperms had large leaves, and that as a result the vascular bundles were disposed in a scattered manner, as is seen in the monocotyledons. He considers that there is in all cases a single terminal cotyledon in the embryo, but that it may split and the halves diverge through 180°. Like the cotyledon, all the leaves are terminal organs, and hence dominate the stem ("grandifoliate"). From this condition has been derived the one in which the stem is dominant and the leaves small ("parvifoliate"). This view of phylogeny naturally leads WORSDELL to reject the evidence derived from the vascular system of seedlings adduced by JEFFREY and others, although he claims to adopt the "recapitulation theory." In the present paper he outlines the results of an extensive study of the leaves in certain representatives of Ranales, and shows how the scattered bundles of a petiole may be converted into a ring, and the bundles of one side of the ring approximate the opposite side so as to produce a single arc.—M. A. CHRYSLER.

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[27] JEFFREY, EDWARD C., Traumatic ray-tracheids in *Cunninghamia sinensis*. Annals of Botany **22**:593–602. *pl. 31*. 1908.

[28] WORSDELL, W. C., A study of the vascular system in certain orders of the Ranales. Annals of Botany **22**:651–682. *pls. 32, 33*. 1908.

Solution of mitoses.—Experiments of OES[29] with various root tips, embryo sacs, and pollen mother cells show that cells capable of growth and division contain a chromatin-dissolving enzyme (*nuclease*), which dissolves chromatin when toluol, chloroform, carbolic acid, etc., are added. Metaphases, anaphases, and telophase are most quickly attacked, the prophases being less susceptible, and the resting nucleus still more resistant. In autolyzed objects the spindle is dissolved, but the nucleolus and nuclear membrane of resting nuclei remain unaffected. The effect of temperature, neutral salts, free acids, and alkalies was observed in various objects. The writer believes that the diminution of chromatin in the telophase, observed by STRASBURGER and others, may be due to nuclease. If nuclease functions in the normal, living plant, thus causing irregular fluctuations in the chromatin, the question arises whether chromatin is the exclusive bearer of hereditary qualities.—CHARLES J. CHAMBERLAIN.

Tyloses in tracheids of Conifers.—CHRYSLER[30] has reinvestigated this subject, and finds tyloses in the heart wood of the root, and in the first year's growth of the axis of the strobilus. So far as his work goes, they are confined to Pinus, the examination of the root wood of 12 other genera and of the cone axes of 7 other genera failing to reveal them. The effect of wounding was also studied, but it did not result in extending the range of tyloses, either to other genera or to other regions of Pinus; but wounding did result in inducing the occurrence of tyloses in the normal regions of Pinus. It is suggested that these facts may provide an additional reason for considering Pinus to be an ancient genus.—J. M. C.

Plant diseases.—STEWART and HODGKISS in a recent bulletin[31] discuss the carnation bud rot previously described by HEALD and WOLCOTT of the Nebraska Experiment Station. It is a disease which is known to occur in New York, Illinois, and Nebraska, and which is attributed to a species Sporotrichum with the association of a species of mite.

The disease of grass known as silver top is also discussed in this same bulletin and attributed to the same fungus in association with the same mite, though the relation of the mite to infection has not been completely worked out in either case.—F. L. STEVENS.

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[29] OES, ADOLF, Ueber die Autolysis der Mitosen. Bot. Zeit. **66**:89–120. *pl. 5.* 1908.

[30] CHRYSLER, M. A., Tyloses in tracheids of Conifers. New Phytol. **7**:198–204. *pl. 5.* 1908.

[31] STEWART, F. C., AND HODGKISS, H. E., Tech. Bull. 7, N. Y. Agric. Exper. Sta. Oct. 19, 1908.

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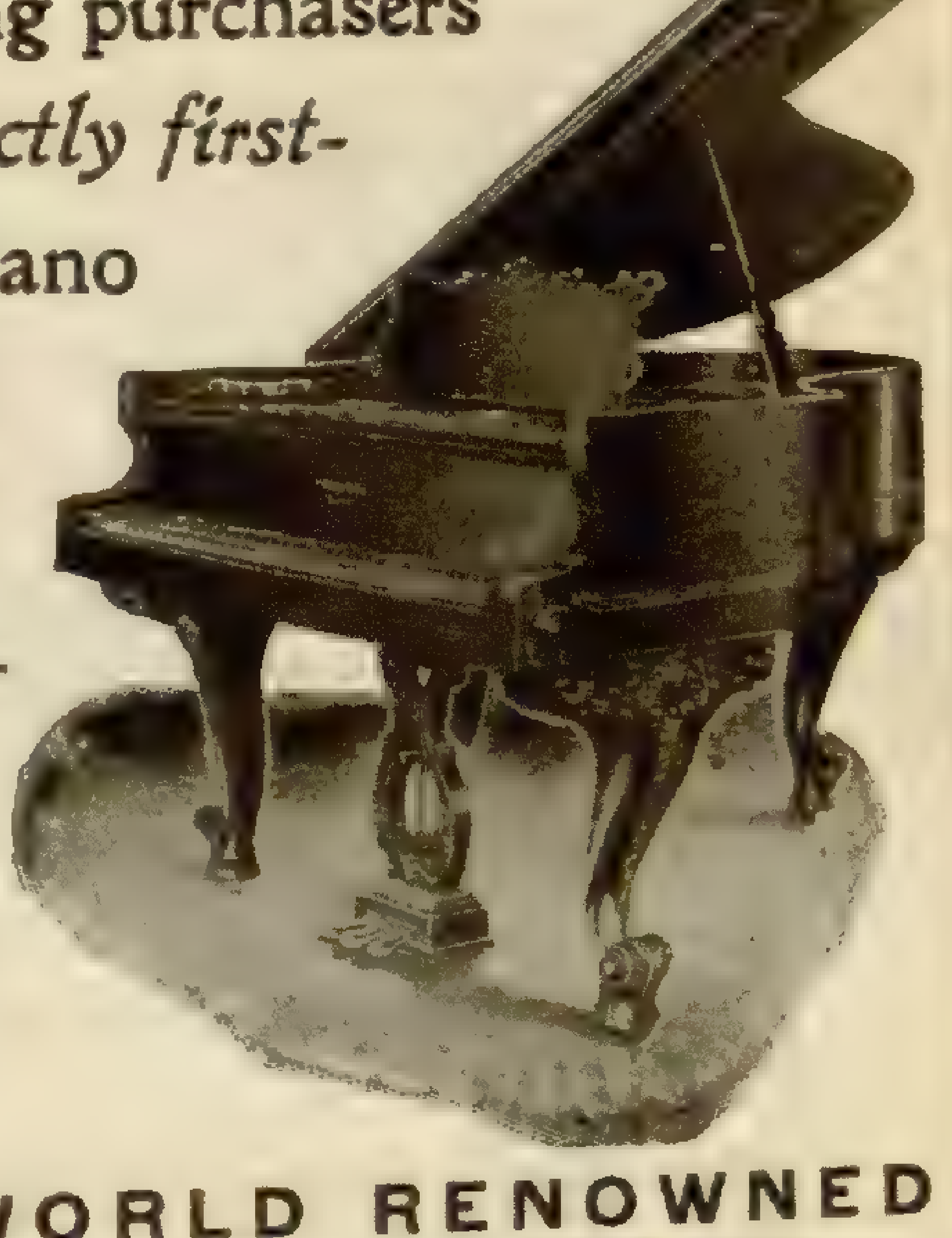

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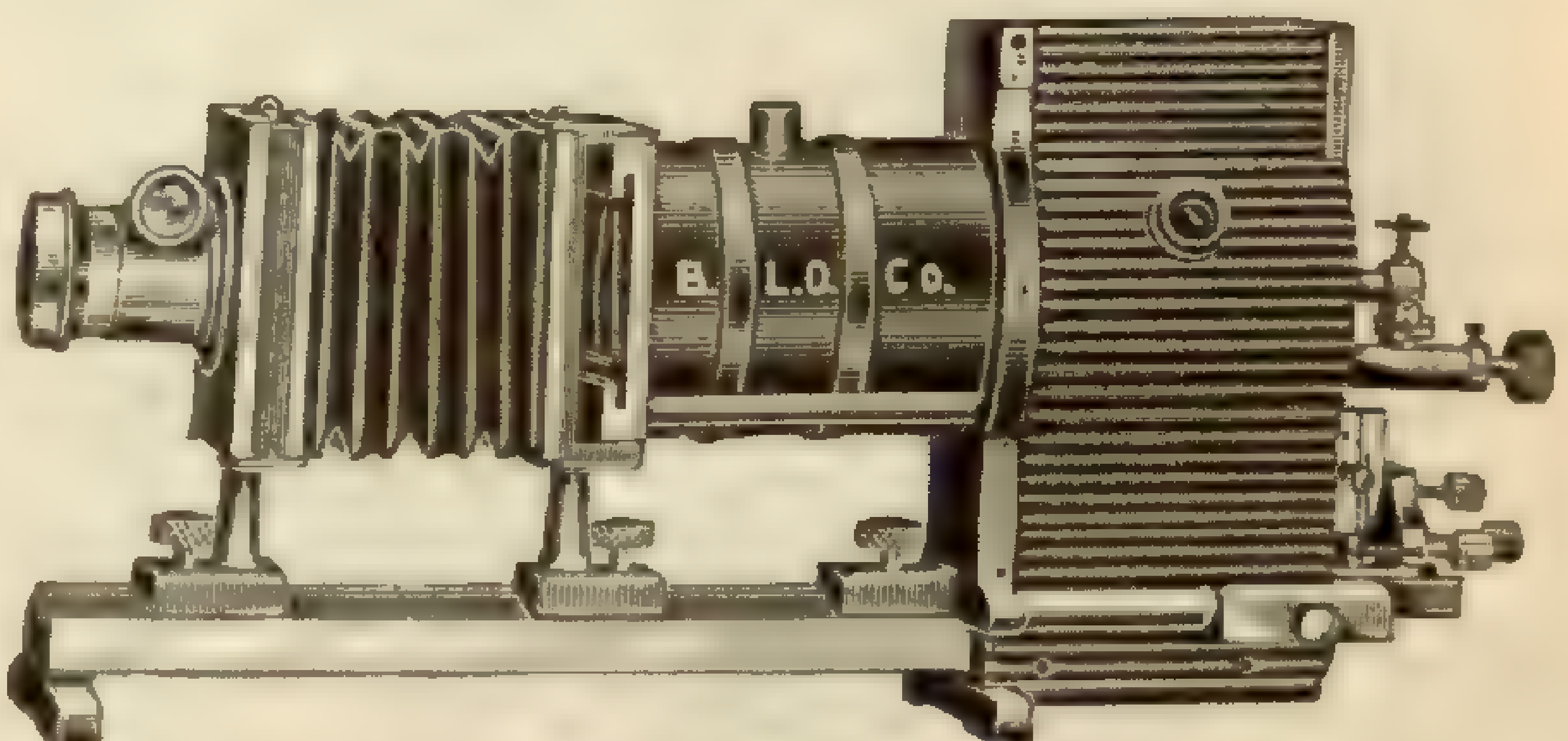

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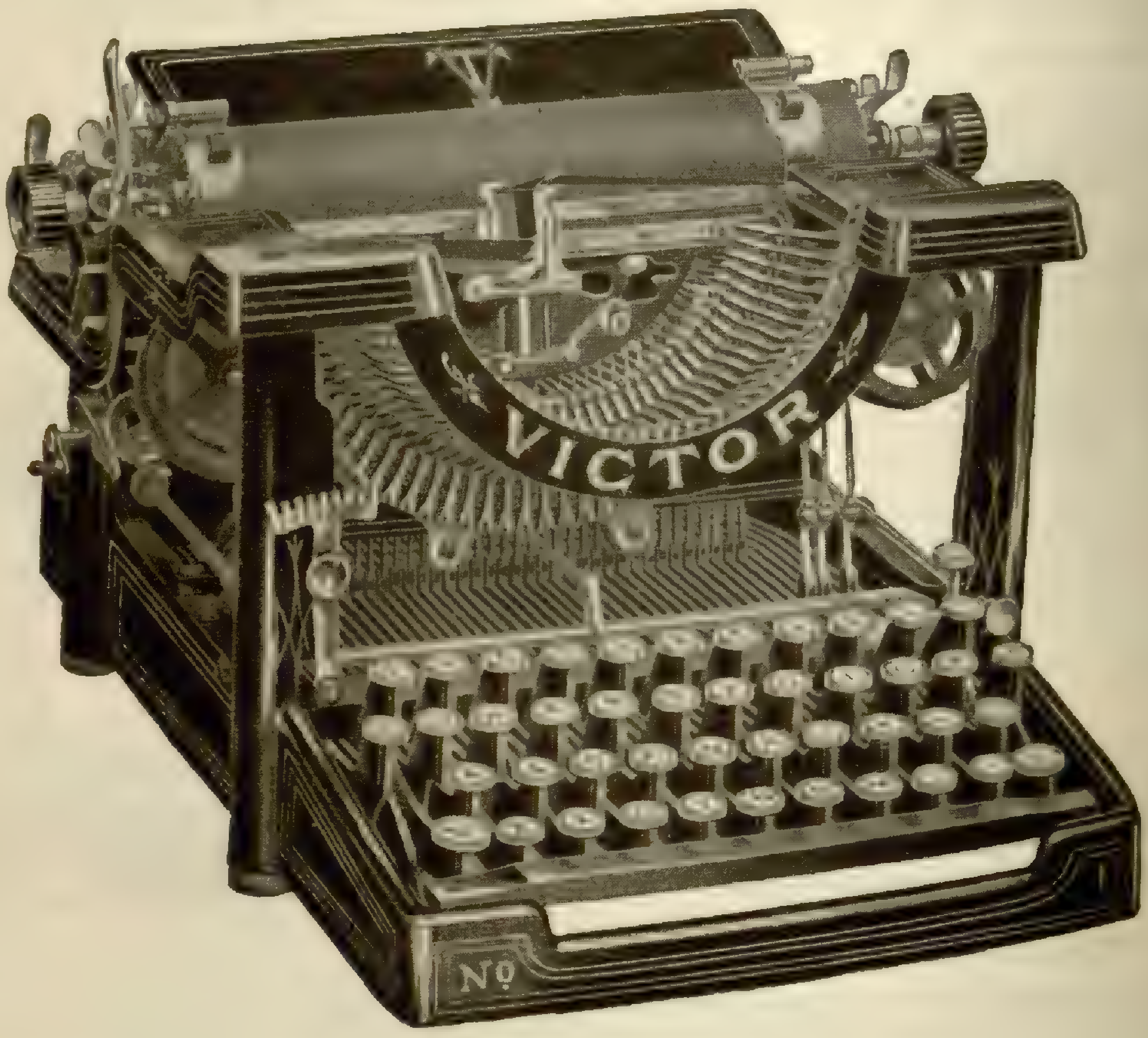

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March 1909

Editors: JOHN M. COULTER and CHARLES R. BARNES

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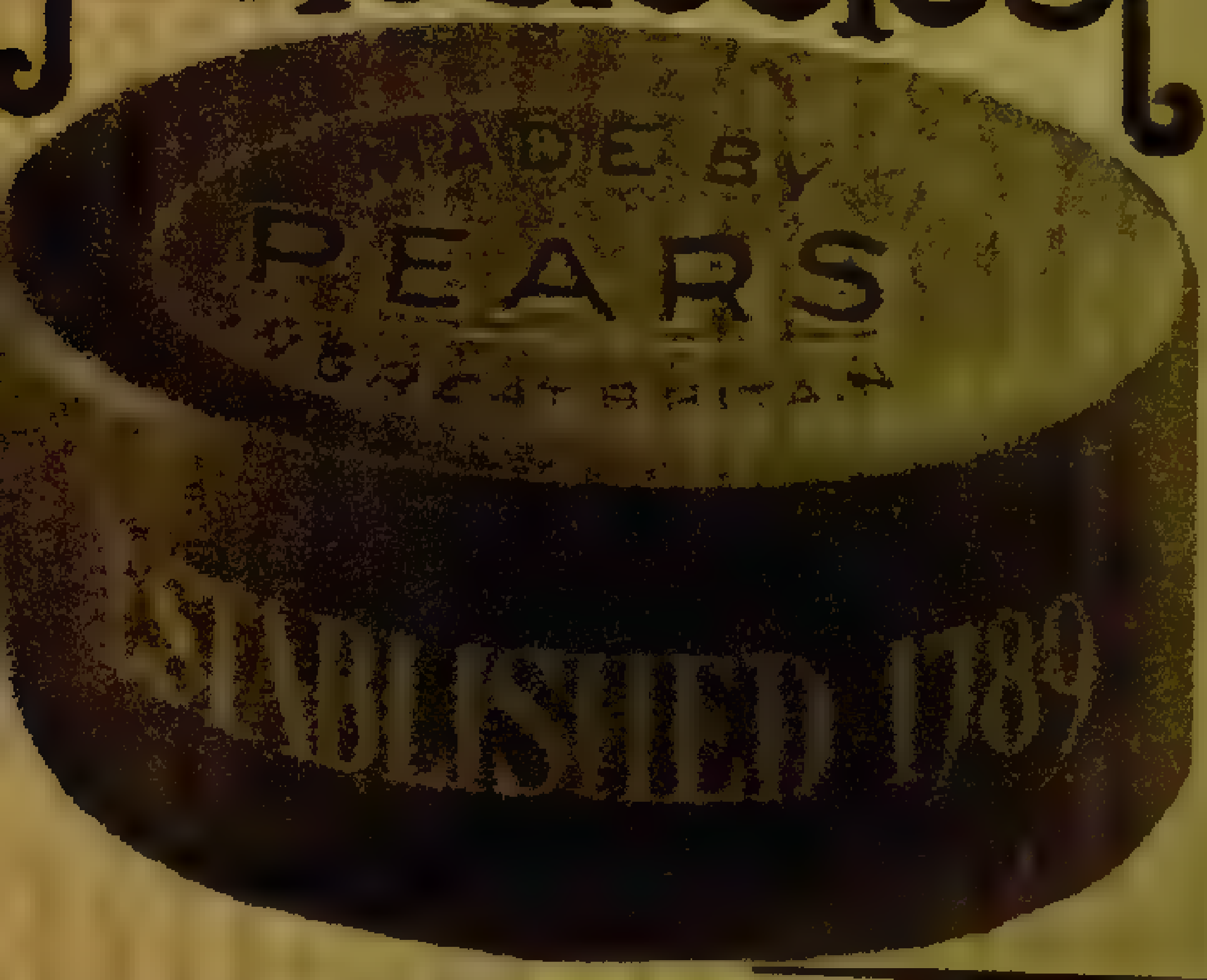

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Vol. XLVII

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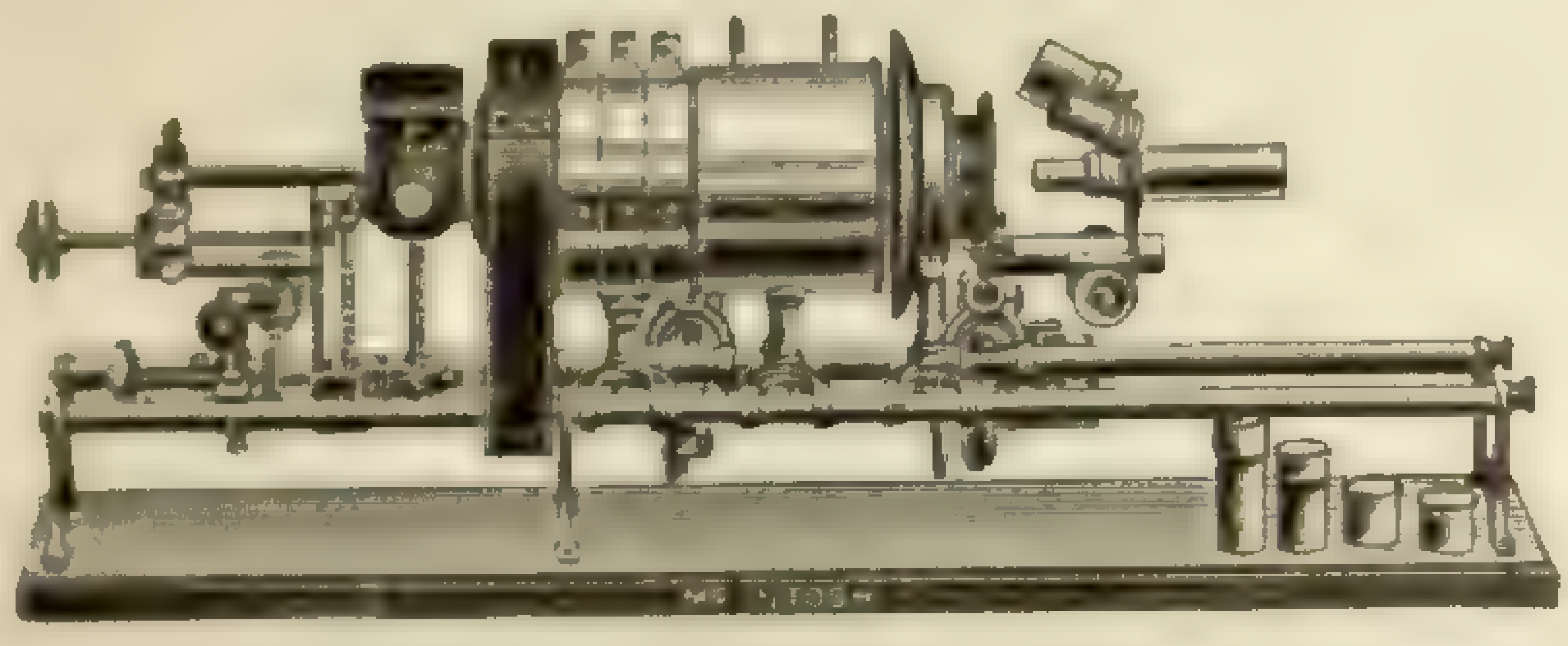

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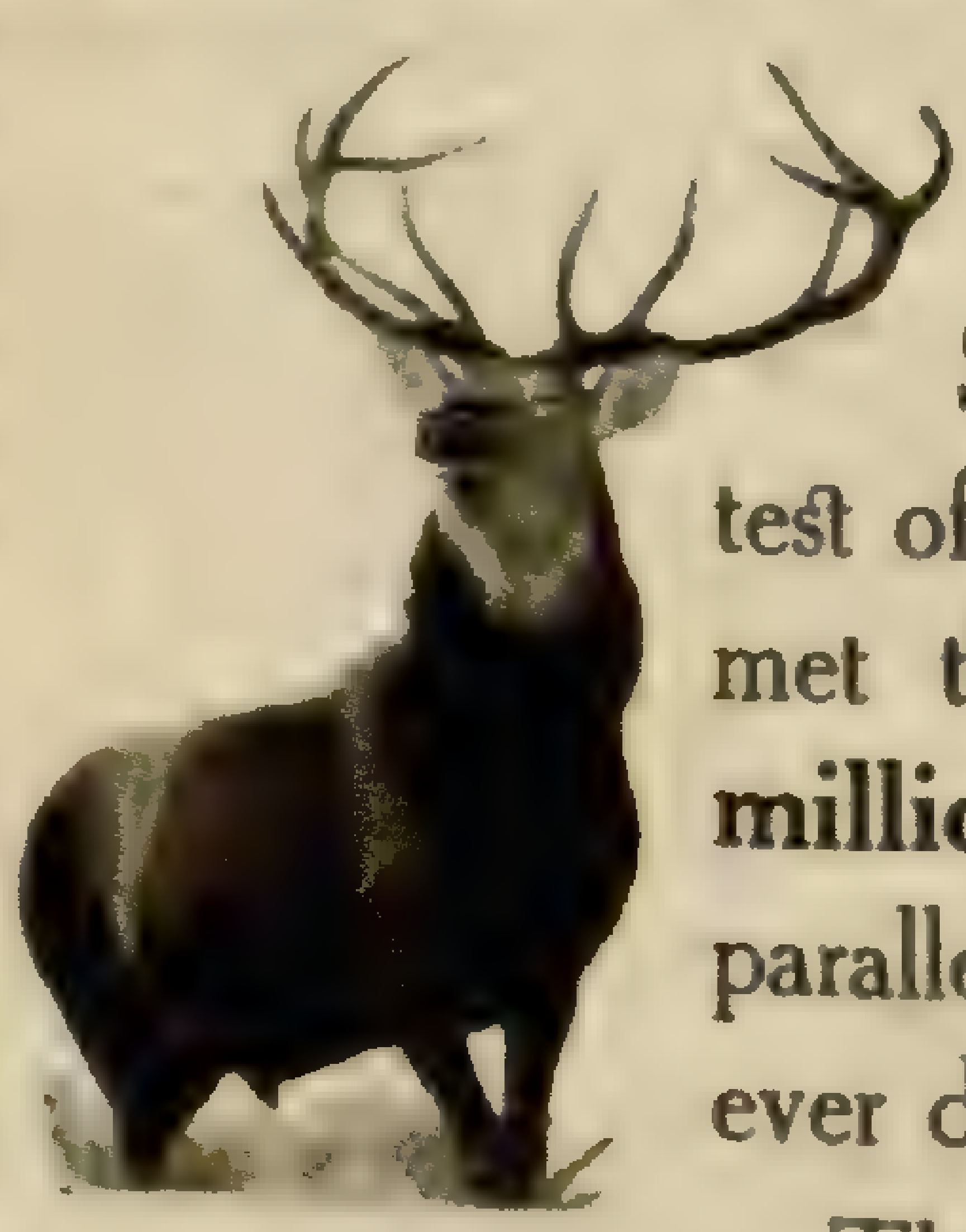

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BOTANICAL GAZETTE

MARCH 1909

MITOSIS IN FUCUS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 124

SHIGÉO YAMANOUCHI

(WITH PLATES VIII–XI)

INTRODUCTION

The first cytological study of Fucus is that of FARMER and WILLIAMS (**8**), published about ten years ago as a preliminary note. The next year STRASBURGER'S paper (**24**) on *Kerntheilung und Befruchtung bei Fucus* appeared. In 1898 the final paper of FARMER and WILLIAMS (**9**) was published.

FARMER and WILLIAMS' material, *Fucus platycarpus*, *F. serratus*, and *F. vesiculosus*, was collected on the coast of England. Their account deals with egg-formation in the oogonium, particular attention being devoted to the third division; also with fertilization and early segmentation divisions. *Ascophyllum nodosum* and *Pelvetia canaliculata* were used in a supplementary way. STRASBURGER'S work was based chiefly on material from Heligoland, Germany; in it he describes in detail the third division in the oogonium of *Fucus platycarpus* and the fertilization processes in *F. serratus* and *F. vesiculosus*.

To the brilliant results of these authors we owe most of our present knowledge of the cytology of these forms. Since the work of FARMER, WILLIAMS, and STRASBURGER, cytological conditions have been studied in a few algae, such as Dictyota (WILLIAMS **27**), Nemalion (WOLFE **28**), and Polysiphonia (YAMANOUCHI **29**). The morphology of chromosomes, in connection with the theoretical problem of alternation of generations, especially in the algae, is becoming a more important problem. For the solution of such a problem, there must be a thorough study of the life-cycle of chromosomes; unfortunately not much of such work has been done in algae. The work of FARMER, WILLIAMS, and STRASBURGER dealt only slightly with the first two mitoses in the oogonium, where it was inferred, but not actually observed, that the reduction of chromosomes takes place. Mitoses in the antheridium, from the first division to the development of mature sperms, were not studied. In the present investigation, special attention is paid to the behavior of chromosomes in the first and second mitoses in the oogonium, and to mitoses in the antheridium.

The results here presented are based upon a study of *Fucus vesiculosus* L. Material was collected and fixed at Woods Hole, Mass., during the latter part of March and early April, 1908. As fixing reagents, Flemming's weak solution containing osmic acid, with various modifications, proved to be most satisfactory. There are several points of interest and importance in regard to the relation between the frequency of mitotic figures and environmental conditions, both in the oogonium and antheridium and in the young thallus. In general, the plants collected one or two hours after being covered by the tide were full of figures. Material was imbedded in paraffin with a melting point a little less than 52° C. Sections were cut 3 μ, sometimes 5 μ thick. Flemming's saffranin and Heidenhain's iron alum hematoxylin, with or without counterstains, were mostly used in the slides from which the accompanying illustrations were made.

To Professors JOHN M. COULTER and CHARLES J. CHAMBERLAIN I am indebted for their kind suggestions and criticism during the progress of this work.

MITOSES IN VEGETATIVE CELLS OF THE THALLUS

Any young part of the thallus, when well fixed, showed figures available for study, especially in the apical region, in the adventitious outgrowths which are not infrequent, and in the early stages of conceptacles or cryptosomata. The nuclei in the thallus, except in cases of young sporelings, are generally very small and difficult to study; but to make certain as to whether the number of chromosomes remains constant in the thallus grown under normal conditions, a thorough study was made of the typical mitoses at various stages of development. The following brief account of the essentials is illustrated by figures from the apical portions of male and female plants. Since the mitoses in male and female plants are precisely alike, the following account may be understood as applicable in either case.

The nuclei in the growing apex of the plant are somewhat larger than those in older regions of the thallus, sometimes filling almost all of the lower half of a narrow elongated palisade cell, such as constitutes the surface layer of the thallus. The cells are filled with an abundance of contents, such as plastids, physodes, and other granular substances of undetermined nature. In regions where such contents are scarce, the cytoplasm shows a very fine alveolar structure, which gradually becomes granular, even, and homogeneous toward the nuclear membrane.

In early prophase the chromatin network of the resting nucleus changes to a structure in which numerous chromatin knots become more and more pronounced, until they become transformed into well-developed chromosomes (*figs. 1a, 1b, 7*). The chromosomes, which at first appear very irregular in size and shape, now become quite similar in form, slightly bent, and in this condition they are arranged in an equatorial plate (*figs. 2, 8*).

During the chromosome development within the nucleus, the cytoplasm has a tendency to become transformed into kinoplasm at the two poles. As a rule in these kinoplasmic accumulations, centrosomes appear first in the late prophase, when the chromosomes are arranged in the equator (*fig. 2*). The nuclear membrane persists generally up to late metaphase, being especially well marked toward the equatorial region. In the polar region where the centrosomes lie, the membrane will perhaps be very faint, so as to allow the developing spindle fibers to intrude into the nuclear cavity while the astral rays are formed outside. Owing to the minuteness of the nucleus, it is rather difficult to make any positive statement in regard to the origin of the centrosome and spindle. These features can be treated more satisfactorily in connection with the divisions in the oogonium and the early segmentations of the fertilized egg.

The number of chromosomes in the early prophase (*figs. 1a, 1b*) is more than 60, but 64 chromosomes can be counted with certainty in the late prophase (*figs. 3, 7*) and anaphase (*figs. 6, 12a, 12b*) in the polar view of the equatorial plate. In metaphase, the chromosomes at the equator split and separate, and in anaphase two sets of daughter chromosomes proceed toward the poles (*figs. 4, 10*). The sets of daughter chromosomes when they reach the poles no longer remain in one plane, but become aggregated into more or less irregular spherical masses which then become vacuolate. Probably through the interaction of the nuclear sap, derived perhaps from the vacuolation, and of the surrounding cytoplasm, a new membrane is organized, thus completing the process of typical mitosis.

The centrosomes that were always observed staining black at the poles lose gradually their sharp identity, until they can no longer be differentiated by stains.

MITOSES IN ANTHERIDIA

In Fucus antheridia develop from wall cells of the conceptacle. A wall cell of the conceptacle puts forth a papilla which is cut off by a transverse wall (*fig. 13*). The papilla grows for a time and divides, forming the antheridium and its stalk (*fig. 14*). A stalk cell may produce again either several antheridia directly or a papilla which gives rise to an antheridium and a stalk; the latter often repeats papilla formation again and again, so that there are produced conspicuous branching systems bearing numerous antheridia.

The young antheridium enlarges after its formation until its length becomes 2–4 times greater than its breadth, the growth of the cell being accompanied by that of its nucleus. The cytoplasm contains deeply staining granules and is very dense, especially in the neighborhood of the nucleus. The nucleus in the resting condition contains a comparatively large amount of chromatin substance arranged in a network evenly distributed throughout the nuclear cavity. At this time neither kinoplasmic accumulations nor centrosomes are differentiated. The nuclear network, composed of ragged chromatin, now becomes transformed into a somewhat thicker thread (*fig. 15*).

This transformation of the chromatin from a fine ragged reticulum to a thread accompanies the first manifestation of polarity in the nucleus; for it does not occur simultaneously throughout the cavity, but is more active near the nuclear membrane. The fine ragged material previously scattered throughout the central portion of the nucleus moves toward the peripheral region and becomes transformed into chromatin threads, leaving the central part of the cavity comparatively free from chromatin (*fig. 16*). The chromatin threads become thicker and an eccentric distribution of them takes place (*fig. 17*), until finally they are grouped in synapsis at one side of the cavity (*fig. 18*).

The chromatin threads, thus eccentrically grouped in synapsis, have a certain regularity, i. e., they are not in a tangled mass or ball, but are in groups of almost parallel loops, converging to a spot where they are attached to the inside of the membrane. While this eccentric synapsis of chromatin threads is going on within the nucleus, in close association with the threads in synapsis, the cytoplasm directly outside the membrane becomes transformed into dense kinoplasm. Not infrequently there are two synaptic groups (*fig. 19*) at two opposite poles within the nucleus; and naturally in such cases two kinoplasmic accumulations appear in association with the two synaptic groups.

The loops grouped in synapsis thicken and shorten, the two arms of each loop touching each other (*figs. 20, 21*). They now condense considerably, appearing therefore a little smaller, and become detached from the spot where they lay during synapsis. Each of these condensed loops becomes a pair of bivalent chromosomes (*fig. 22*). Later, the two halves of such a bivalent chromosome become closely applied to each other, so that the whole chromosome appears to be a small spherical mass. Such is the condition of prophase.

In late prophase a single centrosome appears in the kinoplasmic accumulation at one pole (*fig. 23*), the centrosome at the other pole making its appearance later. Radiations and achromatic spindles develop in connection with the centrosomes. The spindles then attach themselves to the chromosomes and an equatorial plate is established (*fig. 24*).

It is important to note the origin of the chromatin threads or spirem in synapsis and the relation between the spirem and chromosomes. The chromatin threads in synapsis, which have arisen from the transformation of a delicate ragged chromatin reticulum in the resting nucleus of the young antheridium, are not paired, but single. As a consequence, the loops in synapsis are single in nature. An examination of the loops cut transversely during synapsis showed that the arms of the loops are altogether about 64 in number (*fig. 21*). Finally, both ends of the loops being detached, 64 chromosomes are formed, each pair of which, being derived from two arms of a loop, becomes a pair of bivalent chromosomes. The number of these bivalent chromosomes may be readily counted again in the polar view of the equatorial plate (*fig. 25*). When the two halves of a bivalent chromosome begin to separate, the figure (*fig. 26*) shows the characteristic aspect of the heterotypic mitosis. The two sets of the daughter chromosomes then separate and proceed to the poles of the spindle (*figs. 27, 28, 29, 30*). The central spindle is of short duration; when the daughter chromosomes aggregate in a mass and organize a new nucleus, the spindle fibers entirely disappear. The centrosomes disappear at the end of telophase.

The two daughter nuclei, after a short rest, commence the second division, which is simultaneous, the antheridium remaining without much increase in size. In prophase, 32 chromosomes are differentiated from the chromatin reticulum, and in the later part of this phase two centrosomes appear (*figs. 31, 31a*) one after the other; the achromatic spindle is developed in connection with the centrosomes and an intranuclear mitotic figure is established (*figs. 32, 32a*). Metaphase (*fig. 32*), anaphase (*fig. 33*), and telophase in the two nuclei proceed simultaneously and finally four nuclei are formed.

Soon after the telophase, the cytoplasm between the four newly formed nuclei shows a fibrillar arrangement connecting the nuclei, but the display is of short duration and the four nuclei remain either in a group or scattered with no regularity along the longitudinal axis of the antheridium. The second division does not differ much from typical mitosis, except that the nuclear membrane dissolves at an earlier stage in prophase, and that no cell plate is laid down between the daughter nuclei.

The four nuclei in the antheridium, after a short rest, begin the third division, which is accompanied by a gradual growth of the cell. The third division in each of these four nuclei naturally results in eight nuclei (*figs. 34, 34a, 35, 35a, 36, 36a*). The eight nuclei give rise by simultaneous division to sixteen nuclei (*fig. 37*). The fifth division follows at once in each of these sixteen nuclei, resulting in the formation of thirty-two nuclei (*fig. 38*). These simultaneous mitoses take place with only short resting periods between, and precisely the same as the second mitosis. The centrosome is most brilliant at the first mitosis and gradually becomes fainter in the successive divisions. The number of chromosomes in early metaphase (*figs. 34a, 37a, 38a*) and late anaphase (*fig. 36a*) of these mitoses is 32.

The formation of partition walls in the antheridium begins to take place at the 32-nucleate stage. Up to this stage, the nuclei of the antheridium are free, but finally in telophase of the fifth mitosis, with the disappearance of the central spindle in each mitotic figure, there could be seen in the neutral region between any two nuclei the faint manifestation of a protoplasmic plate formed by the transverse walls of fine alveoli becoming perceptibly thicker and arranging themselves in such a way as to appear as an uneven or somewhat zigzag line in section. The unevenly continuous walls of the alveolar lamellae grow gradually thicker, and soon uniform plates are laid down simultaneously, so that the antheridium is divided into 32 cells.

The nuclei in these cells of the antheridium undergo one more mitosis, the sixth, which results in 64 nuclei (*fig. 39*). Thirty-two chromosomes are present at this mitosis (*fig. 39a*). This last division is also accompanied by the laying down of thin protoplasmic partition walls, so that the antheridium now contains 64 cells, which are spermatids or sperm mother cells.

The nuclei in the spermatids undergo a peculiar modification, and with an accompanying change of cytoplasm surrounding the nucleus, there is produced a sperm with two cilia. The details of the events which occur in the antheridium following the 32-celled stage, as well as the development of the sperm from the spermatid, will be treated in a separate paper which will be published later.

MITOSES IN OOGONIA

It is well known that oogonia in Fucus develop from the wall cells of the conceptacle. The wall cell puts forth a papilla which divides into two cells, an oogonium and its stalk. The oogonium enlarges to a considerable size, and three mitoses occur within, naturally producing 8 nuclei, each of which with its cytoplasm becomes an egg.

The mitoses in the oogonium of Fucus have already been studied chiefly in *Fucus platycarpus*, and in a supplementary way in *F. serratus*, by STRASBURGER, and mainly in *F. vesiculosus*, and in a supplementary way in *Ascophyllum nodosum*, by FARMER and WILLIAMS. The detailed accounts given by these authors are devoted chiefly to the last one of the three mitoses, the first and second mitoses being touched only slightly. The following is a description of the first two divisions in the young oogonium in *Fucus vesiculosus.*

The resting nucleus in the oogonium contains a delicate chromatin reticulum which is scattered irregularly throughout the cavity. The amount of chromatin substance seems rather scanty in proportion to the size of the nucleus (*fig. 40*). One or two very large nucleoli generally lie isolated in the center. The cytoplasm in general has a very delicate alveolar structure, which is very frequently interrupted here and there by plastids, physodes, and black-staining spherical bodies of undetermined nature. Toward the periphery of the nucleus, the cytoplasm assumes a mixed structure of fine granules and fibrils. The nuclear membrane seems extremely delicate. No polarity is manifested in this resting condition.

In very early prophase, a ragged chromatin reticulum gradually passes into a thread, at first branched and then becoming simple. As was described for the first mitosis in the antheridium, the transformation of the ragged chromatin into a thread is more active at the periphery of the cavity, so that after a while the chromatin threads are observed running irregularly and more abundantly along the periphery than in the center, thus leaving the center nearly free from chromatin (*figs. 41a, 41b*). When the partial distribution of the chromatin thread proceeds farther, the most of the tangled mass of threads is located at one side of the nuclear cavity (*figs. 41b, 42a, 42b*), showing the beginning of a typical synapsis.

Coordinate with these internuclear changes, kinoplasm develops and accumulates close to the nuclear membrane at a spot where it associates with the synaptic group of the threads within the nucleus. The threads gradually shorten and thicken. The irregularly tangled threads now become regularly arranged into loops. These loops are evidently formed by the folding back repeatedly of long continuous threads, the blunt ends of which protrude toward the cavity, while the opposite ends become closely attached to the nuclear membrane (*figs. 43a, b, c; 44a, b*). The loops are therefore not independent of one another, but are connected also at the base, which is in contact with the membrane in such a way that an arm of one loop, by turning back, passes directly to the arm of the next loop. These connections of the loops at the base are detached and there results a number of loops in synapsis. The number of the loops is not easily counted from profile views; however, a section cut transversely through the loops showed that there are 64 cut ends of arms of the loops (*fig. 45*). Consequently, the number of loops is 32, each loop consisting of two arms.

The loops differ at first in their thickness and length, but by thickening and shortening they gradually become similar, a change which is more rapid in the thinner and longer ones. The loops now become more closely associated with one another during the culmination of synapsis. The two arms of each of these loops in contact with each other gradually become more compact and consequently appear smaller. The two arms of each of these loops then separate at the bend—the point of connection—and form a pair of bivalent chromosomes in prophase of the first division. The bivalent chromosomes remain for a while at the spot where they were grouped in synapsis, and then become distributed in the nuclear cavity (*fig. 46*). Therefore in Fucus, pachynema, strepsinema, and diakinesis stages are very much modified.

Some attention was paid to the centrosome. When the kinoplasmic accumulation is first visible at one pole of the nucleus in early prophase, a small body is differentiated distinctly in the midst of the accumulation, and it soon becomes surrounded by radiations. The centrosome with its radiations is always in association with the synaptic group of loops. When the bivalent chromosomes are scattered throughout the cavity (*figs. 47a, b, c*), a second centrosome makes its appearance, generally at a distance from the first one, sometimes 180° apart from it, but often not so far away (*figs. 49a, b*). The centrosome within the kinoplasm sometimes fragments into two, but then they remain side by side without separating or establishing a new sister centrosome with new radiations. The two centrosomes in the prophase of the first division in the oogonium in Fucus seem to be entirely independent, one appearing after the other. Often the second centrosome has not yet appeared even at a late prophase, when the chromosomes are well organized (*figs. 48a, b*). The radiations seem to increase in number and elongate, probably at the expense of the cytoplasm, as the mitotic process proceeds from prophase to metaphase.

The spindle fibers at first are clearly seen developing from the area surrounding the centrosome, where the nuclear membrane seems to be so thin as to allow the intrusion of the achromatic substance. The rest of the membrane holds its contour very sharply, so that the mitotic figure is intranuclear. Thus the intranuclear spindle of Fucus seems extranuclear in origin.

In late prophase the bivalent chromosomes are arranged in the equator. The nucleolus often remains as a vacuolate structure. The axis of the figure of the first division is variable, either parallel (*fig. 50*) or perpendicular (*fig. 51*) to that of the oogonium. The nuclear membrane, as a rule, dissolves after metaphase, and yet the outline of the figure remains even to late anaphase (*fig. 53*) without the intrusion of the surrounding cytoplasm.

The number of chromosomes in prophase emerging from synapsis is 32, each being bivalent (*figs. 48a, b*). The same number is counted from the polar view of early metaphase (*fig. 52b*). In metaphase, the two halves of the bivalent chromosomes separate. These two halves are not formed by the splitting of one chromosome, but are two independent chromosomes which were two arms of one loop. Later metaphase (*fig. 53*) and anaphase (*fig. 54*) follow; in late anaphase the chromosomes near the pole are straight rod-shaped, without any apparent indication of partition (*fig. 55*). Probably the initiation of the splitting which provides for the second division may be very much delayed in this form. After telophase there are organized two daughter nuclei and the centrosomes become unrecognizable.

The second division in the oogonium follows the first after only a short rest. The differentiation of the chromosomes from the ragged chromatin reticulum and the appearance of centrosomes seem essentially the same as in the typical mitosis. The mitotic processes in the two nuclei, from the beginning to the end, always proceed simultaneously (*figs. 56–62*). In the prophase generally a remnant of the nucleolus is seen at the side of spindle fibers (*fig. 56*) which persists to a late anaphase (*fig. 59*). The relation of the axes of the two figures varies (*fig. 57*). In early metaphase the polar view of the chromosomes in the equator shows the number to be 32 (*fig. 58b*). Anaphase and telophase follow as was described in typical mitosis. The centrosomes always persist with a beautiful display of radiations. When the daughter chromosomes reach the poles and become vacuolate, some of the central spindles seem to be replaced by fibrillar cytoplasm. The cytoplasm between the newly formed nuclei of two sister figures also changes to a fibrillar structure; thus the four nuclei are connected with cytoplasmic fibers (*fig. 63*) that resemble the late telophase of the second division of spore mother cells of some higher plants. Soon after, the fibrillar cytoplasmic structures fade entirely away, and the four daughter nuclei come into close association with one another at the center of the oogonium, and rest for a considerable period. There then follows a rapid growth in the oogonium, which almost reaches its full size before the third division begins.

Detailed descriptions of the third division were given by FARMER, WILLIAMS, and STRASBURGER, and therefore need not be repeated here. A point or two concerning chromosomes seems worth mention. In the early metaphase of the third division, when the chromosomes of a slightly bent rod-shape are arranged in the equator, they take such a position that their long axes lie parallel to the equator without overlapping one another. As a consequence, the profile view of the figure in this stage (*fig. 64*) shows the end view of the chromosomes and the polar view their whole length. It is very easy to demonstrate that there are 32 chromosomes. The chromosomes then split longitudinally in the equator (*fig. 65*), and after keeping their position (*fig. 66*) for a short time, they become directed toward the poles (*fig. 67*), and then the usual anaphase and telophase follow. Therefore the daughter nuclei contain 32 chromosomes.

FERTILIZATION AND THE FIRST SEGMENTATION DIVISION

The events which take place during fertilization as well as during the segmentation division have been described by FARMER, WILLIAMS, and STRASBURGER. Avoiding an unnecessary repetition, a few points concerning the centrosome and chromosomes may be noted.

The resting nucleus of the discharged egg has shown no manifestation of polarity. Cytoplasmic alveolar structures as well as plastids, and spherical globules of various sizes are arranged radially about the nucleus. The cytoplasm surrounding the nuclear membrane has a finely granular aspect. When the sperm has entered the protoplast of the egg and is advancing toward the egg nucleus, a change occurs in the latter. At a certain spot outside the nuclear membrane, there is first observed a dense kinoplasmic accumulation, in which there lies a single deeply staining body very close to the membrane. Faint radiations are formed from the kinoplasm surrounding this centrosome (*figs. 68a, 68b*). The egg nucleus, therefore, is furnished with a single centrosome before the sperm reaches it. The second centrosome has been found to appear in connection with the sperm.

While the sperm is proceeding toward the nucleus, there appear numerous irregularly crowded granules, surrounding the nuclear membrane. The size of these granules at first is not very different from that of the centrosome of earlier occurrence, but they rapidly grow larger and are either spherical or (sometimes) elongated. Their growth, thus, is different from that of the centrosome, so that small granules of the same size as young centrosomes can be distinguished from genuine centrosomes. Such is the condition of the region surrounding the nucleus just before the appearance of the second centrosome. The sperm then reaches the egg nucleus, becomes closely applied to it, and seems to slip in through the nuclear membrane (*fig. 69b*). At this very instant, there is first observed a new centrosome with radiations, appearing at the spot where the sperm entered.

The second centrosome might have been brought in some way by the sperm, as was suggested by STRASBURGER (**24**). Or it is probable that one of the granules surrounding the nucleus might have been brought to the spot mechanically by the streaming movement of kinoplasm caused by the progress of the sperm. At any rate two centrosomes do appear, one after the other, the first one being visible before the entrance of the sperm, and the second arising in connection with the entry. That the appearance of the second centrosome is always associated with the sperm is evidenced by cases of polyspermy (*figs. 76–79*).

Coalescence of the egg and sperm, the entry and progress of the sperm in the egg cytoplasm, and the entry of the sperm into the nucleus, all occur with rapidity. The chromatin of both the sperm and egg nuclei forms the reticulum of the fusion nucleus. The chromatin of both nuclei is mingled so as to become indistinguishable (*figs. 71a, b, c*). The mitoses at the segmentation of normally fertilized eggs (*figs. 72a, b; 73; 74; 75a, b, c*) take place as described by STRASBURGER and by FARMER and WILLIAMS. The number of the chromosomes in the prophase is 64 (*fig. 75a*).

In cases of polyspermy, when two sperms enter the egg nucleus, two centrosomes appear in the two spots where the sperms entered; when three sperms have entered, there are three centrosomes. In case of bispermy there are developed three poles, and in case of trispermy (*fig. 76*) four poles (*fig. 77*) are present; for one pole has already appeared before the sperm enters. In the nucleus with three poles, there are tripolar spindles, and 96 chromosomes become distributed upon the three spindles. The chromosomes split longitudinally at the metaphase, and at telophase two sets of 32 chromosomes meet at each of the three poles to form three daughter nuclei.

In a quadripolar spindle (*fig. 78*) 128 chromosomes are distributed upon six spindles, and each of the four poles receives three sets of daughter chromosomes, numbering 21, 21, and 22 (*fig. 79b*), to form daughter nuclei. In cases of polyspermy, the formation of daughter nuclei occurs simultaneously.

It is very interesting to note that in these cases of polyspermy, the constancy of the number of the chromosomes is maintained by producing multipolar spindles. Whether or not polyspermy may occur in natural conditions has not been determined.

DISCUSSION OF CYTOLOGICAL PHENOMENA

The problem of cilia-bearing structures and centrosomes and their possible relationship is treated best in such a form as Fucus, in which both blepharoplasts and centrosomes are present. As the problem is quite important, it will be treated in detail in the next paper. At present only a brief account of the chromosomes will be given.

Origin of the bivalent chromosomes.—Although the actual segmentation of the chromosomes in Fucus occurs just after the nucleus has emerged from synapsis, their virtual preformation, as continuous chromatin threads from which the chromosomes develop, begins very early in prophase. As was described before, the ragged reticulum of chromatin in the resting nucleus gradually becomes transformed into a thread running in various directions, the transformation being very much more active at the periphery than in the center of the nuclear cavity. The threads in their beginning are uneven and branched, then they become much evener and the transformation continues, so that long continuous threads are formed, running mostly in the peripheral region of the cavity. The threads thus formed seem to have no ends (*fig. 42*), and apparently form one continuous thread. Moreover, any part of the thread shows its single nature from the early beginning of the transformation up to its completion as a continuous structure. Entering into the synaptic condition, the single thread then shortens and thickens, and becomes eccentrically grouped as a loose tangled mass at one side of the nuclear cavity; so that eventually a number of loops are formed by the repeated folding of the thread (*figs. 18, 20, 43, 44*). The loops so developed are therefore still continuous with one another at the bases where they come in contact with the nuclear wall. The loops then become arranged in a loose bunch, parallel and regular, with their bases attached to the nuclear membrane, while the opposite folds protrude into the cavity. Then the loops continue to shorten and thicken and become more and more aggregated; each loop then folds at its bent end so that the bent arms are in contact with each other, when synapsis has reached its culmination. As they emerge from synapsis (*fig. 46*), there are present 32 bivalent chromosomes, which become detached from the nuclear membrane, moving toward the various regions of the nuclear cavity.

The relationship of the chromatin thread in prophase, the loops in synapsis, and the bivalent chromosomes of postsynapsis, may be clearly followed. A pair of bivalent chromosomes corresponds to one of the loops in synapsis; the loops being formed by a folding-back of the chromatin thread, so that a loop in synapsis should be considered as composed of two sporophytic chromosomes arranged end to end. If we apply a modern interpretation of synapsis to this case of Fucus, the chromatin of paternal and maternal origin becomes arranged in early prophase, not in parallel threads, but with the chromosomes end to end, so as to form a single thread, which, passing the so-called leptonema stage, enters into the synaptic condition, during which there probably takes place a close association of the chromatin of the two origins. In this case, the pachynema and strepsinema stages (if they occur at all) must be of very short duration, and consequently the chromatin thread of the zygonema condition in synapsis passes directly into the diakinesis stage. The two elements of the bivalent chromosomes then separate from each other, thus effecting what may be regarded as a reduction. Generally in Fucus the initiation of the longitudinal splitting which provides for the second division does not occur even in late anaphase of the first division, but probably may occur before the organization of the daughter nuclei, as in the generally accepted account of sporogenesis.

Neglecting for a moment the many points which differ in particulars, the results in Fucus, namely, that the chromosomes emerging from synapsis show the reduced number, and that the reduction has taken place by an end-to-end fusion of sporophytic chromosomes, agree in essentials with the views published by FARMER and MOORE (**6**, **7**), SCHAFFNER (**21**, **22**), MOTTIER (**15**, **16**), and STRASBURGER (**25**), and by one group of zoologists, such as VOM RATH (**17**), RÜCKERT (**20**), and MONTGOMERY (**13**, **14**).

Regarding the origin of bivalent chromosomes, however, the author is fully convinced of the correctness of the interpretation that in the majority of cases now investigated, two independent threads originate in early prophase and become associated side by side in synapsis, and that when the two threads emerge from synapsis they form the two elements of the bivalent chromosome. Such cases were clearly established by GRÉGOIRE (**10**, **11**, **12**), BERGHS (**3**, **4**), ALLEN (**1**, **2**), ROSENBERG (**18**, **19**), and some others, including the author himself (**30**, **31**). The author, in a forthcoming paper on sporogenesis in *Osmunda cinnamomea* has reached the same conclusion as has the latter group of investigators. The results in Fucus, however, are not deniable. It is not inconceivable that there are two distinct types of arrangement of sporophytic chromosomes at synapsis.

Constancy in the number of chromosomes.—After the appearance of STRASBURGER'S classical paper (**23**) on "Periodic reduction of the number of chromosomes in the life-history of living organisms," investigators of many forms added to the evidence in favor of the proposed theory. A plant is known to have a certain number of chromosomes, without much variability, in one phase of its life-history. When the number is not too great, an accurate counting is not difficult. The larger the number, however, the more difficult the counting becomes, especially when the chromosomes are long and filamentous, because the stages favorable for exact counting then become more and more narrowly limited.

Unfortunately the rarity of the favorable stages has led some investigators to the hasty conclusion that the counting is almost impossible, while others, being unable to find the favorable stage, have tried to make a rough estimate of the number from such stages as they had. It is no wonder that such rough estimates, based upon stages unfavorable for counting, should vary. It is curious to note that even in *Nephrodium molle*, which contains 66 chromosomes in the gametophyte and 132 in the sporophyte, the number was clearly counted by the author both in apogamous and in normal forms, while FARMER and DIGBY (**5**) claimed that the number of chromosomes varied in the allied forms of *Nephrodium molle* which they studied. The constancy in the number of chromosomes in normal cases has been cited as one of the important proofs of the individuality of the chromosome, and the importance of this theory in any discussion of heredity cannot be neglected.

In the present investigation of *Fucus vesiculosus*, the number of chromosomes was counted in mitoses in the vegetative cells of male and female plants, in the antheridium, in the oogonium, and in sporelings. In the vegetative cells, from the polar view of both early metaphase (*figs. 3, 9*) and anaphase (*figs. 6; 12a, b*), 64 chromosomes were counted. Although the antheridium is very small, the polar view of the mitotic figures in early metaphase showed clearly the same number, as 32 bivalent chromosomes in the first division and 32 univalent chromosomes in the mitoses following the second division. In the first mitosis in the oogonium 32 bivalent chromosomes are present (*figs. 47, 48, 52*) and, as in the antheridium, 32 univalent ones appear in the second (*fig. 58*) and third (*fig. 64*) mitoses. In the first division of the fertilized egg there are 64 chromosomes arranged in the equator. Thus, the number is constantly 32 and 64 in *Fucus vesiculosus.*

FARMER and WILLIAMS (**9**) state that in *Ascophyllum nodosum* the approximate number estimated in the mitotic figure of the oogonium mother cell is about 26–30, and later on they counted in the third division in the oogonium 14–15 as the reduced number. STRASBURGER (**24**) considers 30 to be the probable number in *Fucus platycarpus*, in which he studied chiefly the division in the oogonium. Such a difference in the number of chromosomes in different species of the same genus or in allied forms which grow in normal conditions has also been known in other cases; for instance, in Osmunda, where *Osmunda regalis* has 12 and 24 chromosomes and *O. cinnamomea* 22 and 44.

Alternation of generations.—It has been suggested by STRASBURGER (**26**) that the antheridia and oogonia in young stages (*Anlagen der Oogonien und Antheridien*) should be regarded as corresponding not with antheridia and oogonia of Dictyota but with its tetrasporangia, although the exact phenomena of reduction which occurs in the first two divisions in these structures was not then known in detail. The present result may confirm the correctness of his suggestions.

Briefly summarizing the nuclear conditions of Fucus: The vegetative cells of the plant contain 64 chromosomes, and the same number is present up to the formation of antheridium and oogonium initials. In the first nuclear division in these initials 32 chromosomes appear, the reduced number, but they are bivalent. At the telophase of the second division there are 32 univalent chromosmes. Consequently, the four nuclei resulting from the second division in both oogonium and antheridium initials are the first nuclei which contain 32 univalent chromosomes. Each of the four nuclei divides further within these structures, once in the oogonium and four times in the antheridium, and after the division or divisions there result 8 egg nuclei or 64 sperm nuclei, each nucleus containing 32 chromosomes. At the union of the sperm and egg nuclei, the number is doubled, and the sporeling with the diploid number of chromosomes develops into a Fucus plant.

It would follow that the antheridium and oogonium initials up to the second division may be well compared with spore mother cells in the higher plants, and that the four nuclei in these structures thus produced may be compared with microspores and megaspores, which in Fucus germinate at once within the oogonia and antheridia, and the gametophyte generations, thus initiated, undergo only one mitosis in the oogonium and four mitoses in the antheridium. Thus in Fucus the gametophyte generation with the haploid number extends from the tetranucleate stage both in antheridium and oogonium initials, up to the formation of the sperm and egg. With the union of the gametes, the sporophyte generation with the diploid number of chromosomes begins, and it terminates with the development of the four nuclei in the antheridium and oogonium initials.

SUMMARY

The nuclear conditions during the life-history of *Fucus vesiculosus* may be summarized as follows:

1. The Fucus plant contains 64 chromosomes and the number is reduced at the end of the first two nuclear divisions in the oogonium and antheridium initials.

2. Each of the four nuclei produced at the end of the first two divisions contains 32 univalent chromosomes, and this number persists up to the formation of the sperm and egg; the phase containing 32 chromosomes may be regarded as the gametophyte generation.

3. The union of the gametes doubles the number, and 64 chromosomes are present in every mitosis through the development of the Fucus plant up to the formation of the first four nuclei in the oogonium and antheridium initials. The phase containing 64 chromosomes may be regarded as the sporophyte generation.

4. There is thus present in Fucus an alternation of the gametophyte generation containing 32 chromosomes, with the sporophyte generation containing 64 chromosomes.

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EXPLANATION OF PLATES VIII–XI

The figures were drawn with the aid of an Abbé camera lucida, under Zeiss apochromatic obj. 1.5$^{\text{mm}}$ N. A. 1.30, with compensating ocular 12; except *figs. 1–12, 15–29, 31a, 32a, 34a, 35, 36a, 37a, 38a, 39a*, which were drawn with compensating ocular 18; *figs. 13, 14, 30, 31, 32, 33, 34, 36, 37, 38, 39, 76–79*, drawn with ocular 8; and *figs. 42, 48, 50, 51, 53, 56, 57, 59, 60, 63*, drawn with ocular 4. The plates are reduced to one-half the orginal size.

PLATE VIII

Mitoses in the vegetative cells of the male plant

Figs. *1a, 1b.*—Two sections of the same nucleus in the cortical layer of the thallus; no centrosome has appeared, the nucleus is in early prophase and the approximate number of chromosomes can be estimated from the two sections as near 64.

Fig. 2.—Late prophase: two poles; centrosomes in the center.

Fig. 3.—Stage similar to *fig. 2*, viewed from pole: chromosomes 64.

Fig. 4.—Metaphase: two sets of daughter chromosomes separated.

FIG. 5.—Anaphase: each of the two sets of daughter chromosomes arranged almost in a plane.

FIG. 6.—Stage similar to *fig. 5*, viewed from pole: chromosomes 64.

Mitoses in the vegetative cells of the female plant

FIG. 7.—Early prophase of the nucleus in vegetative cells of the thallus: chromosomes (estimated) about 64.

FIG. 8.—Early metaphase: centrosomes with a few radiations.

FIG. 9.—Stage similar to *fig. 8:* chromosomes 64.

FIG. 10.—Anaphase.

FIG. 11.—Late anaphase.

FIGS. *12a, 12b.*—The same stage as *fig. 11*, viewed from pole: two sets of 64 chromosomes.

Mitoses in antheridia

FIG. 13.—Developing papilla, to become later an antheridium: nucleus approaching prophase.

FIG. 14.—Later stage of papilla: nucleus in anaphase; when this mitosis is completed, there will be formed a stalk cell and an antheridium.

FIG. 15.—Nucleus of the antheridium in resting condition, showing delicate chromatin network: no centrosome.

FIG. 16.—Nucleus with chromatin network beginning to be transformed into a more or less pronounced thread structure: nucleolus without any connection with the network; no centrosome.

FIG. 17.—Nucleus with first indication of polarity: chromatin thread more thickly tangled at one corner of the nuclear cavity; cytoplasm begins to show kinoplasmic nature.

FIG. 18.—Nucleus in synapsis: parallel chromatin loops protrude from one side of nuclear membrane into the nuclear cavity.

FIG. 19.—Nucleus in synapsis: most of the chromatin loops aggregated at two poles; a few threads traverse the nuclear cavity, connecting the poles; this case is rare.

FIG. 20.—Nucleus still in synapsis: the loops thickened and shortened.

FIG. 21.—The same stage, viewed at right angles.

FIG. 22.—Early prophase just after synapsis: chromosomes showing bivalent nature.

FIG. 23.—Prophase: a centrosome at one pole; the two constituents of the bivalent chromosome come in close contact, so its double nature cannot be recognized.

FIG. 24.—Metaphase: a number of chromosomes arranged in the equatorial plate; centrosomes with radiations.

FIG. 25.—The same stage as *fig. 24*, viewed from the pole, showing 32 (in reality bivalent) chromosomes.

FIG. 26.—Late metaphase: bivalent chromosomes in the equatorial plate at the point of separation, revealing characteristic feature of heterotypic mitosis.

FIG. 27.—Anaphase: two sets of daughter chromosomes proceeding toward the poles.

FIG. 28.—Late anaphase.

FIG. 29.—Telophase of the first (heterotypic) division in the antheridium: centrosomes faintly discernible.

FIG. 30.—The antheridium after the first nuclear division: two daughter nuclei in the resting condition; no centrosome.

FIG. 31.—Prophase of second mitosis in the antheridium: two daughter nuclei in similar stage; centrosomes present.

FIG. 31*a*.—One of the two nuclei shown in *fig. 31*, under higher magnification: chromosomes 32.

FIG. 32.—Metaphase: two figures in the same condition.

FIG. 32*a*.—One of the two nuclei shown in *fig. 32*, under higher magnification.

FIG. 33.—Late anaphase: mitosis proceeding simultaneously in the two nuclei.

FIG. 34.—Late prophase of the third nuclear division in the antheridium: four figures in similar condition.

FIG. 34*a*.—One of the four nuclei shown in *fig. 34*, under higher magnification.

FIG. 35.—Metaphase, viewed from the pole: each of the 32 chromosomes has just split.

FIG. 36.—Anaphase: the four nuclei in the same condition.

FIG. 36*a*.—One set of daughter chromosomes from *fig. 36*, under higher magnification: chromosomes 32.

FIG. 37.—Late prophase of the fourth mitosis in the antheridium: eight figures in the same stage.

FIG. 37*a*.—One nucleus in late prophase from *fig. 37*, under higher magnification: chromosomes 32.

FIG. 38.—Late prophase of the fifth mitosis in the antheridium: sixteen figures in similar condition.

FIG. 38*a*.—One nucleus from *fig. 38*, under higher magnification: chromosomes 32.

FIG. 39.—Late prophase of the sixth nuclear division in the antheridium: thirty-two figures in the same stage.

FIG. 39*a*.—One nucleus from *fig. 39*, under higher magnification: chromosomes 32.

PLATE IX

Mitoses in oogonium

FIG. 40.—Resting nucleus of the oogonium: chromatin showing ragged structure and nucleolus without apparent connection with it; no centrosome.

FIGS. 41*a*, 41*b*.—Two sections of the same nucleus in very early prophase: ragged chromatin transformed into a thread; a centrosome has made its appearance with a few radiations.

FIG. 42.—Early stage of synapsis: centrosome with radiations not shown in this figure.

FIG. 42*a*.—Nucleus from *fig. 42*, under higher magnification: chromatin threads very much tangled; centrosome not shown here.

FIGS. 43*a*, 43*b*, 43*c*.—Three sections of the same nucleus in synapsis: chromatin threads in form of loops becoming attached by their ends to a part of the nuclear membrane, outside of which there lies a centrosome with radiations.

FIGS. 44*a*, 44*b*.—Two sections of the same nucleus in synapsis, similar stage to above: there a black staining body associated with a nucleolus.

FIG. 45.—Section through the base of crowded loops, at contact with the nuclear membrane, showing 60 or more isolated chromatin dots, some of them connecting with one another; the dots are either the ends of the loops or their optical sections.

FIG. 46.—Nucleus emerging from synapsis: chromatin loops moving from the place of aggregation in synapsis; two arms of each of these loops are always in close association, forming bivalent chromosomes; centrosome in next section.

FIGS. 47*a*, 47*b*, 47*c*.—Three sections of the same nucleus in prophase: 32 bivalent chromosomes; now two centrosomes lie at two poles, one of the centrosomes being newly formed, independent of the other that appeared at a previous stage; some of spindle fibers beginning to intrude into the nuclear cavity.

FIGS. 48*a*, 48*b*.—Two sections of the same oogonium: 32 bivalent chromosomes; these figures show the case where there is still only one centrosome.

FIGS. 49*a*, 49*b*.—Two sections of the same nucleus in prophase: two poles less than 180° apart; intruding fibers attaching to chromosomes.

FIG. 50.—Early metaphase: intranuclear figure established, its axis parallel to that of oogonium.

FIG. 50*a*.—Intranuclear figure in prophase from *fig. 50*, under higher magnification: remnant of nucleolus still visible near the spindle.

PLATE X

FIG. 51.—Metaphase a little later than the stage in *fig. 50*, with the axis of the figure at right angles to that of the previous one.

FIG. 51*a*.—Nucleus from *fig. 51*, under higher magnification: the nuclear membrane has disappeared.

FIGS. 52*a*, 52*b*, 52*c*.—Three sections of the same nucleus in metaphase: the middle section shows 32 bivalent chromosomes, although their bivalent nature is hardly discernible.

FIG. 53.—Anaphase: the case where the contour of the nucleus still remains undisturbed even after the dissolution of its membrane.

FIG. 54.—Nucleus in anaphase, similar stage to *fig. 53*, under higher magnification.

FIG. 55.—Portion of one set of daughter chromosomes in late anaphase, showing their rod-shape while attached to the spindle fibers.

FIG. 56.—Prophase of the second mitosis in the oogonium: two figures similar.

FIG. 56*a*.—Nucleus from *fig. 56*, under higher magnification: the figure is intranuclear; nucleolus still remains.

FIG. 57.—Oogonium in which two nuclei show early metaphase: two figures perpendicular to each other.

FIG. 57*a*.—One of two figures in *fig. 57*, under higher magnification.

FIGS. 58*a*, 58*b*, 58*c*.—Three sections of the same nucleus in early metaphase: the middle one shows 32 univalent chromosomes in the equatorial plate.

FIG. 59.—Oogonium with two nuclei in early anaphase.

FIG. 59*a*.—Nucleus from *fig. 59*, under higher magnification: nucleolus still remains; two centrosomes still showing conspicuous radiations.

FIG. 60.—Oogonium with two nuclei in late anaphase.

FIG. 60*a*.—Nucleus from *fig. 60*, under higher magnification.

FIG. 61.—Telophase: two centrosomes with their radiations still recognizable; central spindle about to disappear.

FIG. 62.—Late telophase: chromosomes aggregated at poles beginning to vacuolize; meshes of cytoplasm arranged somewhat radially from two poles toward the equator.

FIG. 63.—Section of oogonium cut transversely through its axis, after late telophase of second mitosis: only three of four daughter nuclei are figured; between every two of these three nuclei is an irregular fibrillar arrangement of cytoplasm.

FIG. 64.—Late prophase of the third division, viewed from pole: chromosomes (32) in the equatorial plate before splitting.

FIG. 65.—Metaphase: nuclear membrane still present; most of the chromosomes arranged in the equator show their ends, the stage being just after splitting.

FIG. 66.—Late metaphase: nuclear membrane almost dissolved; daughter chromosomes beginning to separate.

FIG. 67.—Anaphase: nuclear membrane has disappeared, the contour of the spindle-shaped nucleus undisturbed.

PLATE XI

Fertilization and segmentation of fertilized egg

FIGS. 68*a*, 68*b*.—Two sections of the same nucleus in resting condition, from a discharged egg before fertilization, showing delicate ragged chromatin and two nucleoli; a single centrosome close to the nuclear membrane, without any radiations (*fig. 68b*).

FIGS. 69*a*, 69*b*.—Two sections of the same nucleus of an egg when a sperm nucleus has just coalesced with it; *fig. 69b* shows a new centrosome which has appeared at the point of the nuclear membrane where the sperm entered; the other centrosome, of earlier appearance, shown in *fig. 69a*, seems split into two by this time; numerous granules surrounding the nuclear membrane stain deeply.

FIGS. 70*a*, 70*b*.—Two sections of the same nucleus of an egg after coalescence with sperm nucleus, a little later stage than *fig. 69*. The sperm nucleus has begun to disintegrate, a delicate chromatin reticulum of the egg nucleus still remaining in the resting condition.

FIGS. 71*a*, 71*b*, 71*c*.—Three sections of the same fusion nucleus: the disintegrating sperm nucleus has completely mingled with the contents of egg nucleus,

1a
2
3
4
5
6
1b
8
9
10
11
12a
7
12b
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
31a
32
32a
33
36
34a
34
35
36a
37a
37
38
38a
39a
39

YAMANOUCHI on FUCUS

40
41a
41b
42
42a
43a
43b
43c
44a
44b
45
46
47a
47b
47c
48a
48b
49a
49b
50
50a

YAMANOUCHI on FUCUS

51
51
52a
52b
52c
53
54
55
56
56a
57
57a
58a
58b
58c
59
59a
60
60a
61
62
63
64
65
66
67

YAMANOUCHI on FUCUS

68a
68b
69a
69b
70a
70b
71a
71b
71c
72a
72b
73c
74
75a
75b
75c
76
77
78
79
79

YAMANOUCHI on FUCUS

so that there is now a homogeneous chromatin reticulum throughout the whole cavity of the fusion nucleus.

FIGS. 72*a*, 72*b*.—Early prophase of the first division in the fusion nucleus: parts of chromatin threads begin to become pronounced, suggesting prochromosomes.

FIG. 73.—Late prophase.

FIG. 74.—Early metaphase: nuclear membrane has disappeared; chromosomes not yet split.

FIGS. 75*a*, 75*b*, 75*c*.—Same stage as *fig.* 74, cut perpendicular to the axis of the spindle: *fig.* 75*b* shows polar view of 64 chromosomes arranged in the equator.

Cases of polyspermy

FIG. 76.—Nucleus of fertilized egg with three sperms: a centrosome with radiations started in connection with each of the spots where the sperms entered.

FIG. 77.—Early prophase: one of the four poles not shown.

FIG. 78.—Prophase, showing quadripolar spindle: one of the four poles not shown.

FIGS. 79*a*, 79*b*.—Two sections of the nucleus in early metaphase; six equatorial plates shown from various views, one of them showing a polar view with 21 chromosomes.

THE REDUCTION DIVISION IN THE MICROSPOROCYTES OF *AGAVE VIRGINICA*[1]

JOHN H. SCHAFFNER

(WITH PLATES XII–XIV)

This investigation, my fourth on the reduction karyokinesis, was undertaken to test the correctness of my former conclusions on a subject apparently beset with many difficulties, judging from the numerous contradictory reports of various observers. Having obtained a year's leave of absence from the university for travel and study, I prepared suitable material of *Agave virginica* L., which was found very favorable for my purpose. The stamens were collected and killed at various hours of the day during the last week in June and the first in July, 1907, a number of vigorous plants being in bloom on the campus of the Ohio State University. The killing fluid used was a weak chrom-acetic acid solution (0.3 per cent. chromic and 0.7 per cent. acetic in water). After imbedding in paraffin, the sections were cut 10–20 μ thick and stained on the slide. After experimenting with various stains and combinations, Heidenhain's iron-hematoxylin was found satisfactory, while Delafield's hematoxylin and the various safranin combinations gave very poor results. This was probably due to the readiness with which the cytoplasm took up and retained these stains. In the whole investigation great care was taken to have the sections correspond somewhat to the size of the nuclei, for sections too thick or too thin may frequently give misleading figures. The nuclei in the microsporocytes of Agave are comparatively small, 15–20 μ in diameter, so it was possible to obtain rather complete spirems and spindles with rather thin sections.

I am greatly indebted to Professor Dr. HANS SCHINZ, of the University of Zürich, where the major part of the investigation was carried on, for his kindly assistance and courtesy shown me during my stay in his laboratory.

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[1] Contributions from the Botanical Laboratory of Ohio State University, XLII.

INVESTIGATION

Incipient stages of division.—The sporogenous tissue is differentiated very early in the young stamens and all vegetative divisions come to an end long before the earlier stages of the reduction division are apparent in the microsporocytes. There is therefore no danger in Agave of mistaking belated prophases of vegetative divisions for stages of reduction. The nuclei of the incipient sporocytes are quite small (*fig. 1*) and usually contain but one or two nucleoli and a rather coarse chromatin net, in which are prominent dark-staining granules. The cytoplasm is rather dense, with a spongy structure. As the sporocytes grow in size the nucleus enlarges considerably, and at various points in the enlarging net, masses of chromatin material appear (*fig. 2*). Studied in detail the net reveals single chromatin granules lying here and there in the linin meshes, and the clumps of chromatin also show definite granules (*fig. 2a*). These masses do not appear to be of a definite number, but approximate the reduction number of chromosomes. They continue to become more conspicuous as the early stages of division progress, until they have the appearance of true protochromosomes. The meshes of the net at the same time become larger, and the finer branches disappear, being probably withdrawn into the larger threads and masses, like the pseudopodia of a rhizopod. The linin network appears to be the active agent, the granules being merely carried apart or together as the linin is moving. I think that there is no question but that these masses are the "prochromosomes" of OVERTON and STRASBURGER. As stated, they are approximately of the same number as the reduction number of chromosomes. The evidence is strong that they represent pairs of individual chromosomes which are orienting themselves preparatory to the formation of the spirem. Since the massing and lengthening of these structures may not be synchronous, the apparent number need not necessarily agree with the reduction number. At this stage the definite pairing of the individual chromosomes must occur, and it may be that this is the only definite pairing during the whole ontogeny. The number of protochromosomes may also appear greater than the reduction number, for the accumulation may at first be taking place at two or more points of the paired chromosomes. It appears that the chromosomes, extended and spread out like a rhizopod or an amoeba in the chromatin net, mass themselves together as definite individuals, probably in pairs; for thus alone are the later stages of reduction intelligible.

During these early stages the tapetum is in the very beginning of its development. It is therefore of value in helping to determine the exact sequence in the development of the sporocytes. And it is of course evident that if the successive stages cannot be determined with absolute certainty, the whole investigation is vitiated.

After the development of the chromatin masses, they seem to elongate, as is shown to some extent in *fig. 3*, and more perfectly in *fig. 4*. Finally they are stretched out into a very long and delicate continuous spirem, with rather uniformly distributed chromatin granules (*fig. 5*). The masses are probably all connected in series and thus elongate into a continuous delicate strand.

If the individuality of the chromosome is admitted, we may conceive the influence which causes paternal and maternal chromosomes to conjugate in pairs in reduction to be of much the same character as that which induces cells to develop as male and female gametes with subsequent union. This property may develop in the chromosomes only at the reduction stage, and if this were the case, the paternal and maternal units might be indifferent in regard to each other during all the vegetative divisions. The evidence on this point must come from normal crosses rather than from hybrids, where the two chromatins may have such a lack of affinity as not to conjugate at all. The independence of the maternal and paternal chromatin observed in the first few divisions of the fertilized egg is of a negative character. But if the individual chromatin masses are distinct in normal vegetative divisions, the pairing may nevertheless certainly take place at the formation of the protochromosomes. It may be well to insist here that the great extension, branching, and change of shape of the chromosome in the resting nucleus does not necessarily impair its individuality. We may reasonably consider the chromosomes to be individualized bodies, passing through a normal ontogeny and acting somewhat like the zoospores of a coenobic plant like Hydrodictyon or Pediastrum, which develop various properties at definite times to take them through their life cycle. They have a definite form, which recurs from generation to generation, but this is lost during the resting stage, even as the cells of a myxomycete lose their individuality in the plasmodium.

First stages of synizesis.—As soon as the extended and delicate spirem is formed, the nuclei mostly appear in synizesis. There are all types of contraction. The chromatin may stretch across the center of the nuclear cavity (*figs. 6, 8*); it may be contracted at one side with the nucleolus (*fig. 7*); or it may be balled up at one side of the cavity with the nucleolus lying free (*fig. 10*). In some cases the mass is in the center, and often the nuclear membrane is injured by the irregular expansion of the nuclear cavity (*fig. 9*). The period of development during which synizesis occurs is comparatively long, the anther lengthening greatly in the meantime. The anthers of Agave thus make a most favorable object on which to determine definitely the stage when contraction must be looked for in the living material. A thorough study was therefore made of unstained as well as of stained sections, in order that I might become familiar with the appearance of the cells in unfixed anthers.

Study of living cells.—Having ascertained the stage when synizesis occurs in killed material, a study was made of living anthers during the last two weeks in June, 1908, at Columbus. The anthers were examined immediately after removal from the plant. In some cases cross-sections were cut, in others the stamens were cut into short pieces and the sporocyte tissue squeezed out and mounted in water. Both methods were satisfactory. In none of the numerous anthers studied during the two weeks was there the slightest evidence of synizesis. In the great majority of cases the nucleolus is in the center of the nuclear cavity; occasionally it is somewhat to one side; and very rarely near the nuclear wall, as is almost universal in the synizesis of the killed material. The nuclei look large, clear, and vesicular, with granules and flaky material (no doubt the chromatin) scattered throughout the cavity. The synizetic knot would certainly be visible were one present. In the killed material the synizetic mass shows nearly as distinctly in unstained as in stained material. The same undisturbed condition was found in all the cells in every possible stage in the period before chromosome formation. The fact that the nucleoli have a nearly uniform position near the center of the nuclear cavity, while in synizesis they are usually near or against the nuclear wall or flattened out in the "sickle stage," is in itself sufficient proof that synizesis is an artifact. But as stated, the chromatin can also be faintly recognized in the living nuclei, and it should be still more evident if in a contracted ball, since the cavity in typical synizesis is entirely empty of threads, flakes, or granules. The granular material in the nucleus often radiates outward from the nucleolus, and sometimes it is prominently distributed over the surface of the nuclear membrane.

With salt solution and also with 95 per cent. alcohol, the cells contracted considerably and soon became indistinct, so that it was difficult to make out any details. The nuclei were displaced to some extent. The weaker chrom-acetic acid solution, used for the paraffin material, caused the whole mass of sporocytes to contract violently, but not much displacement of the nuclear contents was noticeable. This was probably because the cells were lying rather free and could contract readily from all sides, or the fluid may not have acted long enough. However, it is probable that the synizesis occurs rather suddenly.

An attempt was made to stain the fresh material, both before and after treatment with killing fluids; but this proved unsatisfactory, the stained material showing no more detail then the living cells.

A study of the living microsporocytes of *Agave virginica* indicates that synizesis, as seen in the usual paraffin sections, is an artifact. When the chromatin is comparatively free in the nuclear cavity and is expanding, we find the most decided synizesis. Meanwhile, as will appear further on, synizesis is not confined to this stage, but occurs to a greater or less extent until the chromosomes are fully developed. It is largely on account of the erroneous idea that synizesis occurs at but one stage of division that a number of inaccurate interpretations have been advanced, through which the whole subject of reduction has been confused.

Development of the chromatin loops.—The spirem begins to thicken while the chromatin granules are still in a single row (*figs. 11, 11a*). At this stage synizesis is still frequent, the spirem usually being crowded to one side, but occasionally lying entirely around the nuclear wall (*figs. 12, 13*). The spirem now becomes very distinct, so that it is often possible to trace out great lengths of the thread by focusing properly. It begins to twist into loops and the chromatin granules now appear double (*figs. 14, 14a*). Although the spirem is much thicker at this stage than it was earlier, synizesis is occasionally present, the spirem filling one-half of the nuclear cavity, as shown in *fig. 15*. The double granules are at length prominent, although the spirem does not split (*figs. 16, 16a*). Finally the whole spirem is thrown into definite loops of various shapes and sizes. It is difficult to represent the perspective of these loops in a drawing. One can trace out the position and depth by focusing up and down, but in the camera projection they appear nearly in a plane (*figs. 17–20*). There is no question but that the spirem is continuous, since one can often follow the thread through more than half of the loops without losing the connection, and in uncut sections no free ends are present. In tangential sections or half-sections one can frequently also follow through three or four loops before coming to a free end (*fig. 19*). Practically also, it seems impossible that such twists and loops could be formed unless the spirem were continuous. In *fig. 18a* a number of twisted loops are shown. Some of the loops are produced by a single twist, which results in ring-shaped chromosomes (*fig. 20*). There are three of these ring-chromosomes in the nucleus and they are developed side by side. The three main types of loops are shown in *figs. 20a, 20b*, and *20c*. The loops are not formed, as in Lilium, with a central knot, but more openly. In this stage synizesis was also present in some of the material (*fig. 21*).

After the loops are developed, they are pressed and curved against the nuclear wall, the whole central part of the cavity becoming very hyaline. At the same time they break apart to form the individual reduction or bivalent chromosomes (*figs. 22, 23*). It was exceedingly difficult to determine the number of chromosomes on account of the irregular shapes of those bodies in some nuclei, as appears in *figs. 24, 25*; but it was finally determined that the number is twelve (*figs. 26–32, 37, 38*). In *fig. 26* only fragments of the twelve chromosomes are shown, a large part of the nucleus being cut away.

In cases where the number of chromosomes is said to vary somewhat, the greater or less number may not be of any significance, if the variation appears in vegetative division. Two or more chromosomes might become united through a failure of transverse segmentation, but longitudinal division could proceed in the normal way and the identity of the chromosomes not be lost. But in reduction the number should be definite, if the karyokinesis is to furnish normal cells.

The nucleolus is still present when the chromosomes are fully developed, but often shows signs of fragmentation, as in the examples shown in *fig. 31a*. After the chromosomes are developed, the cytoplasm also shows a change in structure, having passed from a spongy or reticulate arrangement to a more or less radiate structure (*figs. 31, 32*).

Individuality of the chromosomes.—The chromosomes continue to become more indefinite in shape until they appear as irregular, dark-staining, apparently structureless masses, very unequal in size. The real character of the chromosomes can be studied to advantage only during the formative period, although the larger ones can be recognized even in the mother star. In the incipient chromosome loops individuality is very marked. As stated, there are three small ring chromosomes (*figs. 20, 20a, 29, 63*); four large long chromosomes, two of which are very prominently coiled and always side by side (*figs. 20b, 22, 27, 29, 30, 32, 63, 64*); and five smaller chromosomes of various shapes and sizes. Since these are bivalent chromosomes, it is evident that, on the theory of the conjugation of maternal and paternal chromosomes, the conjugating pairs must be quite similar in shape and activity. In the microsporocytes the bivalent chromosomes have an individual shape and size easily distinguishable, and the inference from this is evident, as also in the massing of the chromatin in the early prophase, that these bodies are individualized and retain their individuality from one division to another. Were the chromosomes not individualized, they could not preserve such definite forms and numbers from generation to generation. During its ontogeny, the chromosome passes through a series of forms, only to return, as any other organism, to a definite type at a definite stage. From the present study and the investigations of others, it is evident that the mechanics of chromosome reduction is simple, the usual spirem orienting itself into folds, twists, or simple loops, giving rise to all the various shapes, as rings, rods, coils, tetrads, and crosses. The actual form observed in any individual case may be a mere projection, and great care should be taken to ascertain the actual shape by observation from various points of view.

The spindle and late stages of synizesis.—The incept of the spindle is laid down immediately over the surface of the nuclear membrane while that structure is disappearing. At the same time, connecting lines, which appear prominently in heavy-stained sections, are present, forming a sort of network between the chromosomes (*figs. 37, 38*). The incipient spindle appears as a dense wall of material that was at first mistaken for the modified nuclear membrane, which, however, lies on the inside. This double layer about the nucleus, together with the connecting strands between the chromosomes, makes an ideal arrangement for abnormal contractions, and at this stage there is present a final prominent synizesis of the chromosomes, together with the dissolving nuclear membrane inclosing them. The chromosomes at this stage have not yet fused with the surrounding spindle. A few examples of this appearance are shown in *figs. 32–38*, all about in the same stage of division. Those which show the connecting fibers less distinctly are from the lighter-stained preparations. In fact, without a heavy stain, the connecting threads are barely visible. The contracted nuclei are seen in slides side by side with cells having a normal appearance. There is no doubt in the writer's mind that the phenomenon is an artifact.

The spindle.—The incipient spindle soon begins to show a fibrous character, the fibers at first being few and indistinct, and running more or less parallel toward opposite poles of the nucleus (*fig. 39*). In many cases two more or less pointed caps extend from opposite sides of the nucleus and become prominent before the longitudinal fibers are visible (*figs. 40–42*). The points sometimes show delicate asters, as in *figs. 41, 42*. The spindle fibers develop rapidly, and soon an oval slightly pointed structure is produced, in which the chromosomes and one or more nucleoli lie scattered about (*fig. 43*). The connecting fibers are also prominent, giving the spindle an irregular appearance. The spindle is bipolar from the beginning, originating and developing in the same way as in the vegetative divisions. FULLMER in 1899 showed that in Hemerocallis the spindle originates as a bipolar structure surrounded by a dark zone. This zone was nearly absent in Agave, but the difference may be due to staining. FULLMER showed, however, that the incipient spindle is entirely inside of the dark zone.

The spindle becomes narrower and more pointed and the connecting fibers, apparently contracting while the spindle is lengthening, gradually draw the chromosomes into a perfect circle in the equatorial plane (*figs. 44–60*). In *fig. 48* the spindle is distorted. This was probably produced by the unequal contraction of the cytoplasm. *Figs. 39, 43, 47, 57, 60, 61* make a series, showing how the chromosomes are drawn from their scattered positions into the symmetrical figure of the mother star. A large number of figures of this stage have been included in order to show all the ordinary types of developing spindles to be seen in Agave. In some, the connecting fibers are prominent; in others, especially as the chromosomes approach the equator, one sees only a dark-staining central mass. It is important to note that the spindle fibers appear thickest and densest in their central parts, even in very young spindles. Apparently the chromosomes are attached to the spindle fibers from the beginning. The crowding of the chromosomes against the nuclear wall, as shown in in *figs. 23, 39,* brings the chromosomes into a position where their fusion with the spindle fibers can be accomplished.

The mechanism for bringing the chromosomes from their scattered position into the symmetrical wreath of the mother star is comparatively simple, requiring only the shortening of the connecting fibers, combined with a pull from the spindle threads exerted from the poles. The action of the spindle as well as the attachments must be looked upon as being accomplished by a viscid substance, perhaps under the influence of attractive and repulsive forces. If the substance is contractile in the ordinary sense of the word, it must acquire this property after development.

Multipolar figures.—Multipolar figures were not numerous. This may have been because of the comparatively small size of the nuclei and the thickness of the sections. A special study was made of the multipolar figures found, and the conclusion was reached that they were all artifacts. The various types are shown in the series *figs. 64–73*. *Fig. 64* is a diagonal section, included to show the character and position of the chromosomes in the mother star. Both poles are cut away, one end more than the other. *Figs. 65, 66* are tangential sections representing small parts of the nucleus and spindle. The fibers are both spindle and connecting fibers and make an appearance very much like the figures usually given to represent multipolar spindles. The writer believes that these connecting fibers have caused much trouble in the interpretation of spindle sections. *Fig. 67* might be taken for a tripolar spindle. The few projecting fibers were probably disturbed in the cutting. *Fig. 68* is a spindle broken and distorted by the knife. *Fig. 69* is another torn spindle, the fibers at one end being spread out by the knife. *Fig. 70* has the fibers of one pole cut diagonally. In *fig. 71* one pole is perfect, with a well-developed aster, while the other pole is cut away. In *figs. 72, 73* both poles have been cut off. Such figures are common, as is necessarily the case with cells in which the spindles lie in all directions.

The division of the bivalent chromosomes.—The chromosomes are arranged symmetrically in the mother star (*fig. 61*), with the closed end of the loop extending outward, at least in the long chromosomes (*fig. 61, a, b, c, d, e*). The spindle fibers are attached very near or at the free ends. In the following division the general appearance is entirely different. The larger chromosomes are V-shaped and are attached to the spindle fibers at the head of the V, the two free ends projecting outward (*fig. 62*). The individual character of the chromosomes may occasionally be seen from the polar view, even as late as the mother-star stage (*fig. 63*). The chromosomes are pulled apart very rapidly and are considerably scattered before they reach their new positions in the daughter stars (*figs. 74–77*). In some cells one can see large nucleoli in the cytoplasm along with micronucleoli (*figs. 57–59, 70, 75*).

The daughter chromosomes are arranged in a loose ring or plate, and then begin to contract, until they form a compact dark-staining mass (*figs. 78–82*). In the earlier stages of the daughter star, conditions are again favorable for counting the chromosomes (*fig. 79*), and their smaller size is quite evident when compared with the bivalent chromosomes of the mother star. Delicate radiations are usually visible in all of these stages (*figs. 75–77, 81, 82*).

After the contraction stage of the incipient daughter nuclei, the chromatin begins to expand, the chromosomes putting out pseudopodia-like branches which become more extended until a coarse net is formed (*figs. 83–85*); but even in the oldest daughter nuclei distinguishable before the beginning of the following division, a considerable part of each chromosome persists as an irregular compact mass (*fig. 85*). There is thus in these figures an indication that the individuality of the chromosome is preserved even in the chromatin network.

GENERAL CONSIDERATIONS ON REDUCTION

The important facts brought out in the present investigation confirm a number of conclusions put forward by the writer and others during the past ten years, most of which have been the subject of continual controversy. In a science like cytology so much depends on the manipulation of the material and the interpretation of the figures, that one need not be surprised at the diversity of views held in respect to all the more important cytological problems. In the present paper, by leaving out certain figures in the series, one can produce several of the "reduction processes" heretofore published.

The writer appears to have been the first to present a definite series of observations to show that the first division after pseudo-reduction is the real reduction division. A few previous reports had been published, which were, however, largely guesses or assertions, without definite evidence and sometimes even without drawings.

In 1897, the writer presented his views on the reduction division in the ovules of *Lilium philadelphicum*, advancing the definite conclusions that the spirem is continuous and contains a single row of chromatin granules which later undergo transverse fission; that the continuous spirem doubles up and twists into twelve loops, the reduction number, which then break apart at the inner ends opposite the heads of the loops to form the twelve chromosomes; that during metakinesis the two limbs of the chromosomes are pulled apart, finally breaking at the middle; and that, therefore, there is a transverse division in the first reduction karyokinesis, or a true qualitative division of the chromatin. In that paper *figs. 1, 2, 2a, 4, 4a, 8, 8b, 11, 11b, 12, 15, 21a, 22, 23, 23b, 34, 35* formed a series for which only one interpretation was possible. Only by leaving out *fig. 4* could another interpretation be given, in which case the double spirem appearing later might be considered as conjugating instead of dividing.

In 1901 practically the same results were obtained for Erythronium, and in 1906 for the microsporocytes of *Lilium tigrinum*.

PAULMIER in 1899 showed that in the spermatogenesis of *Anasa tristis* the first division is the reduction division, and more recently MONTGOMERY, in a series of important investigations, has come to the same conclusion. GRIGGS found a reducing division in Ascaris, and observed that the chromosomes are not entirely separated until they are drawn into the equatorial plane.

MOTTIER after a long-continued study of Podophyllum, *Lilium Martagon*, and other plants, has come to conclusions for the most part similar to the writer's, although for many years he held opposite views.

GATES, in a recent article, finds that in the reduction nucleus of the microsporocytes of *Oenothera rubrinervis* the spirem segments transversely into the $2x$ or sporophyte number, and that the members of a pair are thus at first arranged end to end on a single thread. Later the univalent chromosomes are separated, usually in pairs.

It is needless to review the extensive recent literature of reduction, for in many cases the results appear radically different from those presented in this report, and in examining the drawings and conclusions based on them there seems little possibility of harmonizing or explaining the differences.

Finally, it may be said that if any individuality whatever is ascribed to the chromosomes, it becomes evident that they should be arranged end to end to form the spirem, since this is the method in somatic divisions. It is not probable that the cell would develop a fundamentally new method of division in reduction, but rather that such slight changes would be developed in the process as would suffice to bring about the separation of the two sets of chromosomes. The process described in this paper appears to the writer to be the only possible explanation of the figures. As has been stated, however, by making suitable selections, one could represent almost any of the various reduction karyokineses that have been described.

SUMMARY

1. The resting nucleus in the microsporocytes of *Agave virginica* contains a linin network in which small chromatin granules are held, either separate or in lumps.

2. At the beginning of division, the chromatin granules are massed

together through the massing of the linin into a number of lumps corresponding approximately to the reduced number of chromosomes. These masses probably represent bivalent protochromosomes.

3. The masses are all united and elongate greatly until a very delicate, continuous spirem is produced, holding a single row of chromatin granules.

4. After the delicate spirem stage the nuclei in killed material are usually in synizesis. There is no union of two spirems in synizesis.

5. In living material no synizesis is evident, and the nucleoli are not crowded against the nuclear wall, but usually have a central position in the nuclear cavity. Synizesis at this as well as at later stages is an artifact.

6. The spirem shortens and thickens while the chromatin granules undergo transverse division. It finally orients itself into twelve loops of different shapes and sizes.

7. The loops are pressed close to the nuclear membrane, forming a rather definite wreathlike circle, and do not radiate from a closely entangled central mass as in Lilium.

8. The twelve loops break apart, forming the twelve chromosomes —four very large, long, twisted chromosomes; three ring-shaped chromosomes; and five smaller, irregular, more or less bean-shaped chromosomes.

9. The chromosomes are united by connecting fibers, which apparently contract and draw the scattered chromosomes into the equatorial plane while the spindle is elongating.

10. One or two nucleoli are usually present, which are still normal in appearance after the spindle is far advanced in development. The nucleoli are sometimes thrown out bodily into the cytoplasm.

11. The spindle originates as a more or less fibrous layer over the surface of the nuclear membrane before that body dissolves, and at this stage decided synizesis of the chromatin is often present.

12. The spindle is bipolar from the first, with no accessory smaller poles, the poles appearing at first as two, more or less pointed, dome-shaped caps, much the same as in vegetative karyokinesis.

13. The spindle fibers are usually most prominent and thickest in the middle, even in the early stages. There are commonly definite asters at the poles.

14. The multipolar spindles observed are explained as artifacts, mostly produced by cutting.

15. The chromosomes divide transversely during metakinesis.

16. In the daughter nuclei, irregular masses of chromatin persist into the resting condition. These masses represent parts of the twelve daughter chromosomes.

17. In the second division the chromosomes divide longitudinally.

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EXPLANATION OF PLATES XII–XIV

The plates are reduced five-eighths in reproduction. *Figs. 2a, 11a, 14a, 16a, 17a, 18a, 20a, 20b, 20c* were drawn with a compensating ocular 18 and oil immersion objective $\frac{1}{12}$; all the rest with a compensating ocular 12 and oil immersion objective $\frac{1}{12}$, the latter combination having a magnification on the table of 2250.

PLATE XII

FIG. 1.—Microsporocyte showing resting chromatin network.

FIG. 2.—Microsporocyte at a later stage showing masses of chromatin granules in the net.

FIG. 2*a*.—A small portion of the chromatin net showing the linin and massing of the granules.

FIG. 3.—A nucleus with prominent massing of the chromatin into rather definite bodies, protochromosomes.

FIG. 4.—Later stage; the chromatin masses stretching out into a definite spirem.

FIG. 5.—The delicate slender spirem complete.

FIG. 6.—Somewhat older than *fig. 5;* synizesis of the spirem in the middle of the nuclear cavity.

FIGS. 7–10.—Other types of synizesis of the same stage as *fig. 6;* in *fig. 9* the nuclear cavity is expanded.

FIG. 11.—Nucleus with spirem becoming thicker

FIG. 11*a*.—Single chromatin threads from *fig. 11*, showing the light-staining linin with a single row of chromatin granules

FIGS. 12, 13.—Types of synizesis in a later stage than those of *figs. 6–10.*

FIG. 14.—Continuous spirem beginning to fall into loops, showing chromatin granules enlarged and partly double.

FIG. 14*a*.—A short piece of the spirem from *fig. 14*, showing the double nature of the chromatin granules.

FIG. 15.—Same stage as *fig. 14*, showing one-sided synizesis of the continuous spirem.

FIG. 16.—Beginning of the looped spirem, showing further thickening and doubling of the chromatin granules.

FIG. 16*a*.—Pieces of the spirem from *fig. 16*, showing double rows of chromatin granules and distinct linin.

FIG. 17.—Continuous spirem, much thickened and thrown into twisted loops.

FIG. 17*a*.—Pieces of the spirem showing the method of looping and twisting.

FIG. 18.—Microsporocyte somewhat later than *fig. 17*, showing further thickening of the thread and development of the chromatin loops.

FIG. 18*a*.—A number of chromatin loops before the breaking of the spirem.

FIG. 19.—Section of microsporocyte in which several loops can be followed out; the section represents nearly half of the spirem.

FIG. 20.—Beginning of the broken skein stage; the chromosomes beginning to break apart; three ring-chromosomes still connected.

FIGS. 20*a*, 20*b*, 20*c*.—Three complete chromosomes just after the breaking of the spirem.

FIG. 21.—Synizesis in microsporocyte at time of separation of chromosomes.

FIG. 22.—Nucleus with chromosomes completely separated; nuclear membrane still present.

FIG. 23.—Somewhat later stage; chromosomes all crowded against the nuclear wall with a clear cavity in the center.

FIGS. 24, 25.—Nuclei showing indefinite chromosomes.

FIG. 26.—Section of nucleus showing parts of twelve chromosomes.

FIGS. 27, 28.—Nuclei showing twelve chromosomes of diverse shapes and sizes.

FIG. 29.—Section of nucleus showing the three ring-chromosomes.

PLATE XIII

FIGS. 30, 31.—Nuclei with twelve chromosomes, showing the beginning of the appearance of delicate connecting fibers.

FIG. 31*a*.—Fragmenting nucleoli taken from same stages as *fig. 31*.

FIGS. 32–36.—Microsporocytes showing synizesis after the formation of the chromosomes; also connecting fibers between the chromosomes.

FIG. 37.—Nucleus contracted away from the incipient spindle; prominent connecting fibers between the chromosomes.

FIG. 38.—The same, but with less synizesis of the nucleus.

FIG. 39.—Nucleus showing distinctly the incipient spindle.

FIG. 40.—Incept of spindle showing as two caps on opposite sides of the nucleus.

FIG. 41.—Nucleus showing incipient spindle.

FIG. 42.—Nucleus with incept of spindle and aster at one pole.

FIG. 43.—Nucleus showing young spindle and connecting fibers between the chromosomes.

FIGS. 44–46.—Further successive stages in the development of the spindle.

FIG. 47.—Chromosomes, connected by fibers, being drawn into the equatorial plane; spindle with aster showing at one pole.

FIG. 48.—Distorted spindle.

FIG. 49.—Spindle showing the two poles.

FIGS. 50–59.—Successive stages in the development of the spindle and the shifting of the chromosomes into the equatorial plane. *Figs. 57–59* on *plate XIV*.

PLATE XIV

FIG. 60.—Spindle, showing asters and centrosomes; the chromosomes nearly in the equatorial plane.

FIG. 61.—Mother star with aster at the poles.

FIGS. 61*a*, 61*b*, 61*c*, 61*d*, 61*e*.—Chromosomes on the spindle fibers, showing that the closed loop extends outward.

FIG. 62.—A chromosome from the mother star of the second division with the free ends of the V projecting outward.

FIG. 63.—Polar view of chromosomes, showing the three ring-chromosomes; four long chromosomes, two of which lie side by side and are very large; and five smaller chromosomes of various shapes and sizes.

FIG. 64.—Diagonal section of mother star, showing the twelve chromosomes, three of which occupy a central position; also the four long chromosomes.

FIG. 65.—A tangential section of a young spindle, showing spindle and connecting fibers.

FIG. 66.—Tangential section of a spindle, making a multipolar figure.

FIG. 67.—Section showing tripolar figure.

FIG. 68.—Section showing spindle torn by the knife.

FIG. 69.—Torn section, showing spindle fibers cut and spread apart by the knife.

FIG. 70.—Spindle with poles cut away showing two large nucleoli in the cytoplasm outside of the spindle.

FIG. 71.—Spindle, showing pole and aster at one end, the other pole being cut away.

FIG. 72.—Spindle with both poles cut off.

FIG. 73.—Another spindle with both poles cut.

FIG. 74.—Spindle showing first stage of metakinesis, the two large chromosomes being to one side.

FIG. 75.—Metakinesis stage.

FIG. 76.—First stage of daughter star, showing the separated chromosomes.

FIG. 77.—Daughter star stage.

FIG. 78.—Late daughter stars.

FIG. 79.—Daughter star, showing the twelve small chromosomes.

FIG. 80.—Loose daughter skein stage, showing the beginning of contraction of the chromosomes.

FIG. 81.—Daughter skein, showing the close massing of the chromatin.

FIG. 82.—Daughter skein, showing close massing of the chromosomes below the pole.

FIG. 83.—Beginning of formation of daughter net, showing the irregular daughter chromosomes.

FIG. 84.—Further development of the daughter net.

FIG. 85.—Resting stage of daughter nucleus, the chromosomes being still evident as irregular masses.

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J.H.S.

SCHAFFNER on AGAVE

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SCHAFFNER on AGAVE

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SCHAFFNER on AGAVE

SPERMATOGENESIS IN DIOON EDULE[1]

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 125

CHARLES J. CHAMBERLAIN

(WITH PLATES XV–XVIII AND THREE FIGURES)

In March, 1904, and again in September, 1906, the writer visited Mexico for the purpose of studying the Mexican cycads and collecting material for morphological work. The field study was greatly facilitated by the active cooperation of Governor TEODORO A. DEHESA, whose active interest in education has done so much to raise the educational standard of the State of Vera Cruz. I am also deeply indebted to Mr. ALEXANDER M. GAW, of the State Bureau of Information, Xalapa, Mexico. Mr. GAW not only supervised the collection of material and forwarded it to me, but on several occasions visited localities where *Dioon edule* grows and sent me valuable field notes with the collections. The material was collected at Chavarrillo, Mexico, the locality which furnished material for my account of the ovule and female gametophyte of *Dioon edule*.

THE STAMINATE CONE

In March the ovulate cones which were pollinated the previous September have reached their mature size, but the staminate cones from which they were pollinated have disintegrated. Both the ovulate and the staminate cones which are to appear a few months later are still hidden in buds which cannot be distinguished from leaf buds.

Until they reach a length of about 10^{cm} the staminate cones are completely hidden by large bud scales which are fleshy and very hairy, so that the whole structure looks like a moderate-sized ovulate cone. The surface of the cone at this time is densely covered with whitish hairs, which become darker when the cone emerges from the protecting scales.

In September the staminate cones reach their mature size and shed their pollen. Just before the pollen is shed, the cone is firm and erect (*fig. 1*) and measures 10 to 20^{cm} in length and 7 to 11^{cm} in diameter. At the time of shedding the pollen, the axis of the cone elongates considerably and becomes so weak that it bends over until its tip rests upon the leaves of the crown. Insects are very numerous in nearly all the mature staminate cones, but none were found on the ovulate cones, and although the insects were throughly dusted with pollen, there was nothing further to indicate that any pollination was being effected through their agency.

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[1] Investigation prosecuted with the aid of a grant from the Botanical Society of America.

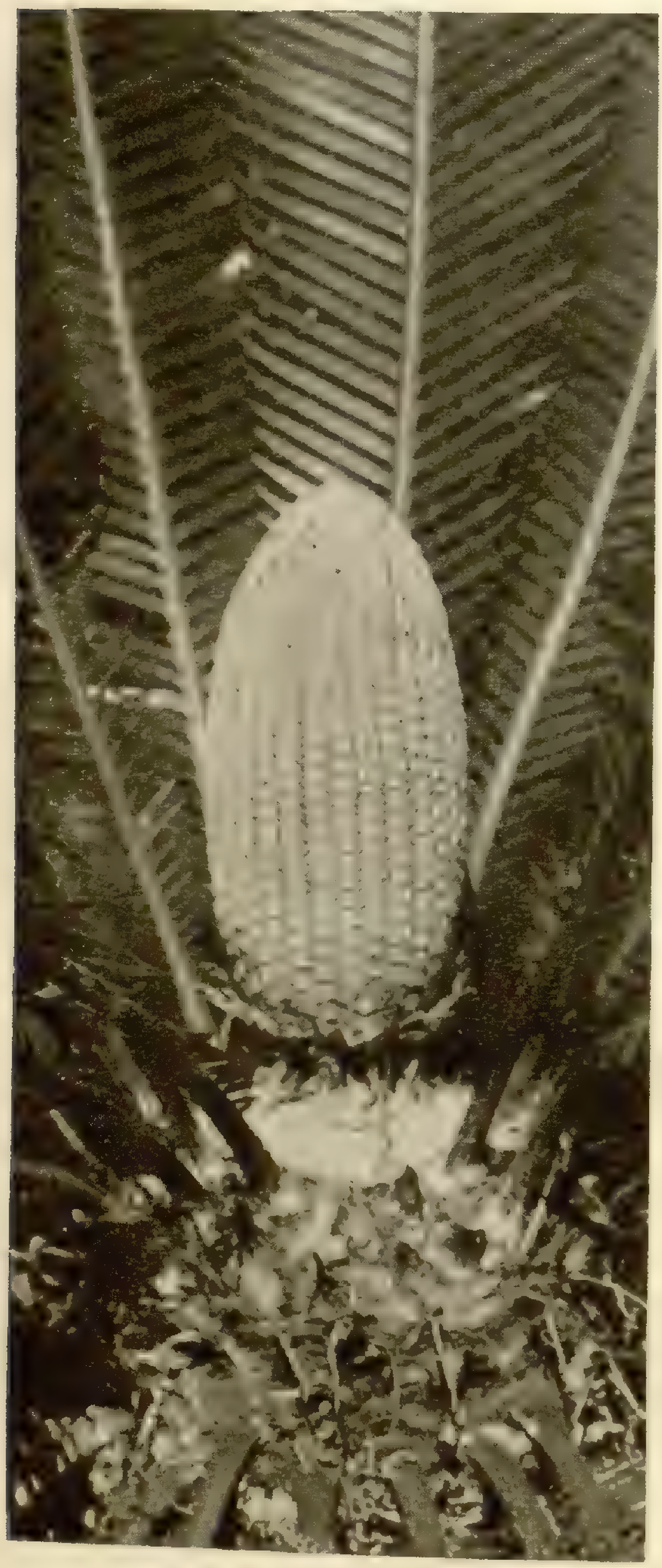

FIG. 1.—Upper portion of plant of *Dioon edule* with staminate cone. Photographed at Chavarrillo, Mexico, September, 1906. One-third natural size.

MICROSPORANGIA

The staminate sporophylls are long and wedge-shaped and end in a single sharp point which curves upward (*fig. 2*). The outer, exposed, abaxial faces of the sporophylls are densely hairy, but the upper faces are quite smooth. In the sporophylls of the upper and lower portions of the cone, a sterile line divides the sporangia into two groups (*fig. 2*), while in the median portions the sporangia cover the entire under surface. The sporophylls are so crowded in the cone that the sporangia on the under side of a sporophyll make a distinct impression upon the upper side of the sporophyll immediately below it.

The number of sporangia on the larger sporophylls varies from about 100 to 300; but the smaller sporophylls bear fewer, and the sporophylls at the apex and base of the cone may bear only a few sporangia, or even none at all.

The sporangia are grouped in definite sori, usually of four or five sporangia, as shown in *fig. 2*. At the stage shown in this figure the line of dehiscence is quite obvious. As the sporangia dehisce, the grouping into sori becomes less obvious. The pollen does not escape immediately, but for a short time is held together in a spherical mass by the scanty remains of the hypodermal wall layers. A hand lens shows that each sorus is surrounded by hairs which grow out from the peripheral portion of the base of the sorus. Many hairs also grow out from the peripheral portions of the sporangia, but there are none in the interior of the sorus, either upon the sporangia or upon the sporophyll (*fig. 4*).

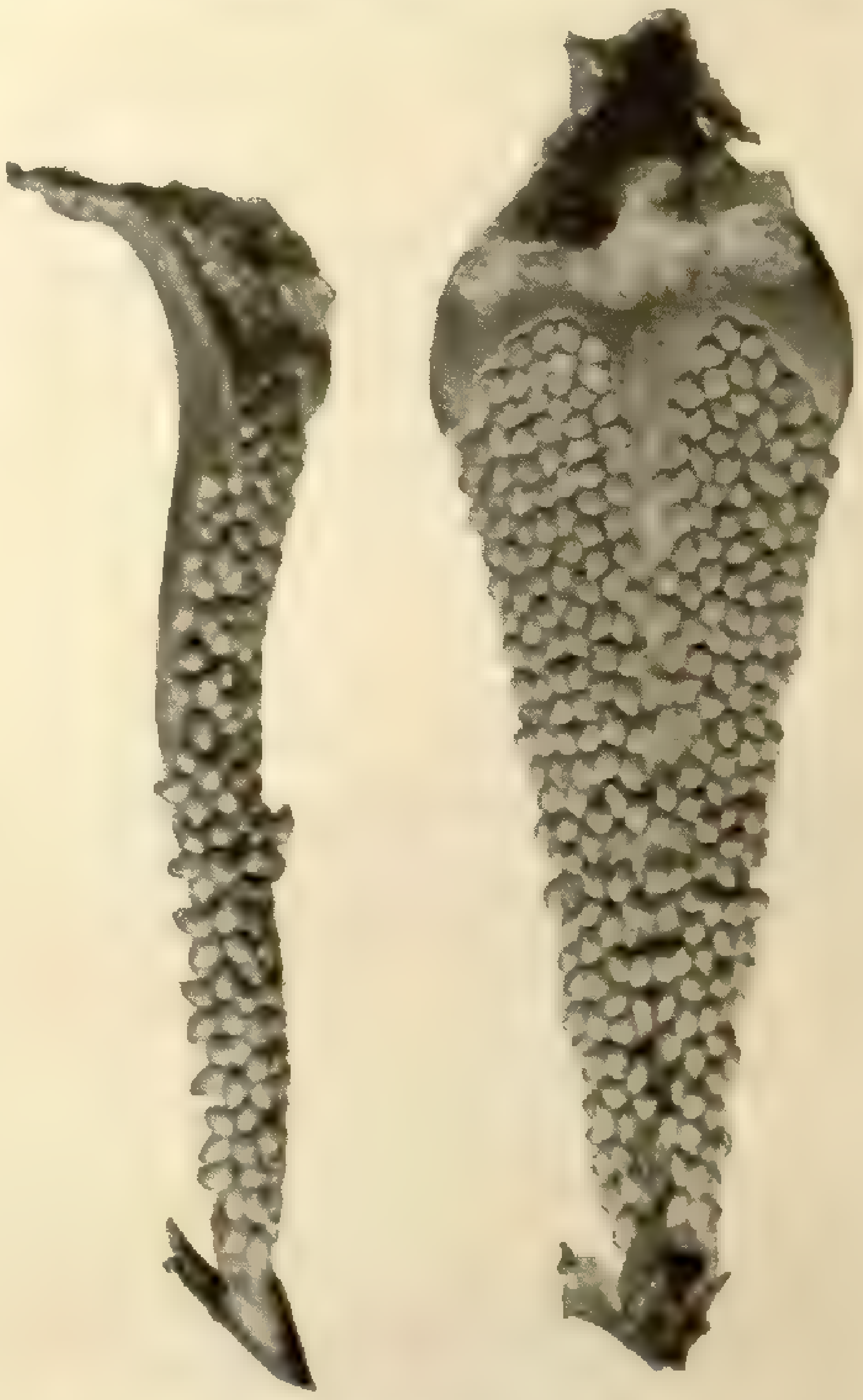

FIG. 2.—Photographs of two microsporophylls of *Dioon edule*. $\times \frac{4}{5}$.

The sporangia are either sessile or have short massive stalks. The stalks and even the lower portions of the sporangia of a sorus may be somewhat united, but there is not so much crowding or so much union as shown by Miss SMITH (**8**) for Zamia and Ceratozamia. The dehiscence, in surface view and in section, is about as figured by Miss SMITH (**8**) for Zamia and Encephalartos.

The general appearance of a sporophyll in transverse section, with its mucilage ducts, vascular bundles, and sori, is shown in *fig. 3*. A more detailed view of two of the sporangia of a sorus is seen in *fig. 4*, which shows the usual amount of union at the base of the sorus. The hairs, especially those which come from the sporangia, are often so numerous and crowded that in transverse section they look more like a parenchyma tissue of angular cells than like sections of tubular hairs.

The hairs do not branch and seldom consist of more than two cells, which are sometimes empty and sometimes filled with a deeply staining substance like that in the epidermal cells of the sporangium.

The wall of the sporangium is composed of three distinct regions, the epidermis, the tapetum, and the intervening wall layers. The epidermis, which is thicker in the upper half of the sporangium than in the lower, consists of thick-walled cells with rather scanty protoplasm, but with an abundance of suberin and tannin. The tapetum, in comparison with the size of the sporangium, is very insignificant, consisting of a single layer of small cells, with occasional patches two cells in thickness (*fig. 5*). The portion of the sporangium wall facing the center of the sorus is noticeably thinner than the wall of the opposite portions, there being four or five layers of cells between the tapetum and epidermis in the former case, while in the latter there may be as many as eight layers (*fig. 4*). The structure of the sporangium from the epidermis down to the sporogenous tissue is shown in more detail in *fig. 5*.

MICROSPORE MOTHER CELLS

The microspore mother cells of Dioon present some peculiarities which are worthy of mention. Upon becoming dissociated, they seldom assume the usual spherical contour, but remain more or less angular, and are nearly always elongated. The chromatin is abundant, but not always well defined, and it is not unusual for the entire nucleus to stain a dense homogeneous black with iron alum hematoxylin, as if chromatin had gone into solution in the nuclear sap. In such cases, there are in the cytoplasm irregular masses of similarly staining material which take the spherical form and begin to resemble nucleoli as the homogeneous staining of the nucleus ceases and the chromatin becomes definitely outlined. When these spherical bodies were first observed, an effort was made to connect them with the blepharoplast, but it was easily determined that they were formed by the rounding-off of the irregular masses, and that they are never surrounded by radiations. They vary in number and position, but this may be true of young blepharoplasts. While the origin of the masses was not determined absolutely, there is little doubt that they represent a portion of the deeply staining material which has passed from the interior of the nucleus into the cytoplasm.

The behavior of the chromatin during the two mitoses by which four spores are formed from the mother cell will be described at some future time; at present I merely note that the number of chromosomes in both mitoses is 12. A hasty examination might lead one to suspect that the number is much larger, since it is not difficult to find prophases of the first mitosis, just before the disappearance of the nuclear membrane, showing any number of chromosomes from 12 to 24. But when there are more than 12, some are always about half the full size. Any number beyond 12 is due to the early separation of the two parts of the chromosome, which, in most cases, are separated only after the chromosomes have become arranged in the equatorial plate. Even in prophase, there are occasional indications of the second splitting which is to be completed at the metaphase of the second mitosis.

These mitoses are not simultaneous throughout the whole sporangium, but begin at the periphery and proceed toward the center, so that there may be a zone of dividing cells surrounding mother cells which are still in the resting condition.

POLLEN BEFORE SHEDDING

The young pollen grains are not quite spherical, there being a flattened portion which might be called the base of the grain (*fig. 6*). The exine is thickest in this basal region, while at the opposite end of the grain where the pollen tube is to emerge, it is very thin. The intine is thinnest in the basal region where it is in contact with the thickest portion of the exine. On the sides of the spore, the intine is very thick, often thicker than the exine. There is no trace of a third spore coat, as described by FERGUSON (**4**) for Pinus.

The microspore germinates while still in the sporangium. A single persistent prothallial cell is formed, lenticular in shape and closely applied to the base of the spore. WEBBER (**2**) described two prothallial cells in Zamia, the first formed being evanescent and the second persistent, but a reexamination by Miss GRACE SMITH (**8**) showed only one. We find only one prothallial cell in Dioon, Zamia, and Encephalartos, and it is persistent. In later stages, after the pollen tube has begun to form, it would be easy to misinterpret, for the line of union of the stalk cell with the persistent prothallial cell often gives the impression of a small prothallial cell beneath the large persistent one (*figs. 10–12*). The illusion is emphasized by the fact that deeply staining granules simulating a broken-down nucleus are sometimes found at the base of the prothallial cell (*fig. 15*). It seems probable that a misinterpretation of this sort was responsible for the description of an evanescent prothallial cell.

The nucleus in the main body of the grain now divides again, the mitosis resulting in the formation of a tube cell and a cell which resembles the prothallial cell and becomes so closely applied to it that the two look as if they had arisen by the division of the prothallial cell (*figs. 7–9*). This cell, so closely associated with the prothallial cell, has been called the generative cell. It soon divides, giving rise to the stalk and body cells (*fig. 10*). The tube nucleus, even before the formation of the tube, increases greatly in size, and the cell which is to form the pollen tube becomes filled with large starch grains. Late in September the pollen is shed in this three-celled condition.

The output of spores can be estimated with reasonable accuracy by the formula $\frac{4}{3}\pi R^3$ = the number of spores in a sporangium. To apply the formula, it is necessary only to count the number of spores in a line from the center of the sporangium to the tapetum, substitute this number for R, and then make the calculation. Of course, this assumes that the mass of spores is spherical and that all spores develop, both of which assumptions are more or less incorrect, but the error is easily less than the variation in the output of individual sporangia of average size. In a few cases, spores were actually counted in a series of sections and the results were practically identical with the estimates by the formula. In the larger sporangia there are about 20 spores in a radius, and consequently the output is about 33,507 spores. The largest sporangia, with a radius of 22 spores, would have an output of 44,600 spores. In some of the smaller sporangia, which nevertheless produce good spores, the output may fall as low as 8000 spores. About 30,000 spores may be regarded as a typical output for the average sporangium of *Dioon edule*.

Late in September or early in October, when the pollen is shed, a large pollination drop, of the appearance and consistency of glycerin, oozes from the micropyle of the ovule. As the pollen passes through the drop into the pollen chamber, at least a portion of the drop becomes brownish and so hard that it adds to the difficulty of sectioning.

THE POLLEN TUBE

Whether in artificial cultures or in the nucellus of the ovule, the pollen tube begins to grow at once, emerging from the apex of the spore and growing out into the sugar solution or into the tissues of the nucellus. The tubes are irregular in diameter and sometimes have short branches, but they are nearly straight and lie so close to the surface that their position is indicated by brown lines radiating from the beak (*figs. 19, 23*). Since the haustorial portion of the tube reaches a length of 2 or 3^{mm}, the brown lines are easily visible to the naked eye. As the tube begins to form, the pollen grain end is pushed into the pollen chamber before the haustorial end has penetrated far into the tissues of the nucellus. The tube is formed from the intine, which breaks through the exine and increases greatly in thickness, as may be seen by noting the comparative thickness of exine and intine in *figs. 8* and *18*. The difference is even greater than is indicated by the figures, because *fig. 8* is more highly magnified than *fig. 18*. The tube stains a light brown with iron alum hematoxylin, contrasting sharply with the brilliant red which the exine takes when stained with safranin.

Starch is abundant in the pollen tube, and filaments looking like the radiations about the blepharoplast, only much longer, are conspicuous, especially in the vicinity of the nucleus.

THE BODY CELL

The division of the generative cell, giving rise to a stalk cell and a body cell, takes place soon after the pollen is shed, all material collected later than the middle of October showing this division already completed.

In characteristic cycad fashion, the prothallial cell now pushes up into the stalk cell (*figs. 10, 11, 12, 15, 18*). Stages between *figs. 9* and *10*, which might show the cause of this peculiar and remarkably constant behavior of the prothallial cell, were not available.

The body cell, which is to produce two sperms, does not divide until the following spring. The division usually takes place about the first of April, but may occur a week earlier, or as late as the first week in May. During this period of about half a year, there is a gradual growth and differentiation of the body cell.

At first the cytoplasm of the body cell seems homogeneous, without any vacuoles or conspicuous granules (*fig. 10*). The chromatin and nucleoli of its nucleus stain sharply with iron alum hematoxylin. Most of the chromatin is in the form of deeply staining granules.

In a short time it is noticed that the nucleus no longer stains sharply, the reticulum appearing very faint, and even the nucleolus and larger chromatin granules taking scarcely any stain. But while these changes are taking place within the nucleus, many granules, staining sharply with iron alum hematoxylin and apparently identical with the chromatin granules, appear in the cytoplasm. For the sake of reference we may call them the *black granules* (*bg*, *figs. 13, 14*). I believe that they have come from the nucleus. Whether the granules pass through the membrane bodily, or become dissolved and pass through by osmosis, might be a question. Living chromatin is semi-fluid and the nuclear membrane at this time is extremely thin. If the nuclear membrane is formed by the condensation of cytoplasm about the nuclear vacuole, the "breaking-down" of the membrane in the prophase of mitosis may be merely the return of the condensed cytoplasm to the ordinary alveolar condition; and as this condition approaches, but while the membrane is still recognizable, it is reasonable to suppose that particles may pass from the nucleus to the cytoplasm without becoming soluble. The black granules might pass from the nucleus to the cytoplasm in this way. There is little doubt that chromatin is more or less soluble. In solution, the granules could pass by osmosis through a membrane with such a structure as a physiologist might imagine the nuclear membrane to have.

The black granules are very small at first and are more numerous near the nucleus. They increase in size by imbibing liquid from the surrounding cytoplasm, until the granule becomes a thin pellicle inclosing a liquid. As the pellicle stretches, granules pass through it into the watery interior, and the color with iron alum hematoxylin gradually changes from black to gray. For reference, these globules may be called *gray bodies* (*gb*, *figs. 14, 17*). Both the black granules and gray bodies are found not only in the body cell, but also in the stalk and prothallial cells, and even in the cells of the nucellus.

THE BLEPHAROPLAST

The origin of the blepharoplast is not easy to determine. In Zamia, Cycas, and Ginkgo, the blepharoplast, when first recognizable, is a small sharply staining granule in the cytoplasm of the body cell. We must admit that the same is true of Dioon, but a study of the black granules led us to surmise that blepharoplasts, in their origin, are simply these granules derived from the nucleus. It would follow that not two but several blepharoplasts might begin to develop. Why only two should become differentiated is not clear. The blepharoplast, in all the early stages of its development, takes an intense homogeneous black color with iron alum hematoxylin, never behaving like the gray bodies. Sometimes the cytoplasm about one or more black granules becomes dense and homogeneous, quite unlike the usual alveolar structure, and resembling the archoplasm which surrounds young centrosomes (*fig. 13*). It is possible that blepharoplasts may begin their growth in this way.

After enlarging considerably, two blepharoplasts become unmistakable through their influence upon the surrounding cytoplasm, which takes on a radiate arrangement with the blepharoplast as a center (*figs. 15, 16*). At first, the radiations are nothing more than the intersections of alveoli (*fig. 16*), but as the walls of the alveoli become less distinct, the radiations become definite granular filaments, extending from the blepharoplast to the periphery of the cell. Many of the filaments are simple, but branching is very common (*figs. 17, 22*).

The appearance of the filaments in preparations indicates a streaming movement, especially toward the blepharoplast. That the radiations seen in sections are streams of cytoplasm is indicated by the fact that exactly similar structures are found in the pollen tube, where there is certainly a strong streaming movement. An almost positive proof that the filaments are streams of cytoplasm is furnished by artifacts. In cutting out the top of the female gametophyte with its archegonia, the least pressure will cause some of the cytoplasm of the eggs to be squeezed out through the necks of the archegonia. This escaping cytoplasm, streaming out through the neck of the archegonium, shows very numerous filaments with a structure identical with that of the radiations about the blepharoplast, and in case of the artifact there is no doubt that the filaments are nothing but streams of the egg cytoplasm. In many cases the connection of the radiations with the blepharoplast also indicates a streaming (*fig. 21*).

Soon after the stages shown in *figs. 16* and *17*, the filaments appear very granular, some of the granules being almost certainly the black granules. The gray bodies become attached to the filaments and give the radiations about the blepharoplast a striking appearance (*figs. 18, 20, 21, 31*). The general topography of the pollen tubes, pollen chamber, and nucellus at this time is shown in *fig. 19*.

The watery gray body runs along the filament, usually in both directions, so that it becomes spindle-shaped, but often it spreads only in one direction, and consequently becomes top-shaped. As the gray bodies spread along the filament, depositing granular matter and giving up their watery content, the filaments become smoothly and sharply defined and have much greater density (*figs. 21, 24*). The growth of the blepharoplast is due, in great measure, to the acquisition of granules, and perhaps other matter, brought to it by the streaming filaments.

During the early stages of its growth, the body cell elongates and the two blepharoplasts with their conspicuous radiations lie in the plane of the long axis, one above and the other below the nucleus (*fig. 18*). The pollen tube, at this time, is very narrow, and this fact may account for the elongation of the body cell, which fills nearly the entire diameter of the tube.

In March the pollen tube has become very large, especially the free end of it, which projects into the pollen chamber, and with this increase in the diameter of the tube the body cell changes from an elongated to a nearly spherical form, the blepharoplasts at the same time rotating 90°, so that they become transverse to the long axis of the tube (*fig. 25*).

Even before assuming the transverse orientation, the blepharoplasts may begin to show vacuolation (*fig. 22*), but after the transverse orientation has become established, the vacuoles become so large and so numerous that they occupy nearly the entire body of the blepharoplast (*fig. 25*). They are scarcely affected by staining, in nearly all preparations showing a dirty-white or pale-yellowish color. The ground substance of the blepharoplast still continues to stain black with iron alum hematoxylin, or red with safranin.

The blepharoplast, when nearly mature, is spherical and measures 16 to 18 μ in diameter. Just before breaking up into granules, it becomes somewhat elliptical in section, with its longer axis parallel with the longitudinal axis of the body cell. The longer axis of the blepharoplast then measures about 20 μ.

THE SPERMS

The body cell divides longitudinally, giving rise to two sperm mother cells (*fig. 26a*). At about the time of this division, the blepharoplast breaks up into a large number of granules, which at first occupy the elliptical area of the blepharoplast. The granules are derived not only from the rim of the blepharoplast but from the portions between adjacent vacuoles. It is possible that granules may also be formed from the radiations, for these begin to disappear at this time. The area of granules soon becomes elongated, and the spiral band begins to appear (*figs. 26*, *26a*). By this time the pollen chamber has extended until it has destroyed all that part of the nucellus lying above the archegonial chamber, so that there is no obstruction between the ends of the pollen tubes and the necks of the archegonia (cf. *figs. 19* and *23*). If the nucellus be removed, the numerous pollen tubes protruding from the pollen chamber are easily visible to the naked eye, and a little later the sperms may be observed without even the aid of a pocket lens (*figs. 27*). In this figure, the star-shaped area is a portion of the tissue of the nucellus, exposed by the rupturing of the megaspore membrane. The evenly dotted portion represents the megaspore membrane, which in this region adheres to the nucellus rather than to the female gametophyte.

As we have said, the spiral band begins to appear as soon as the area of granules elongates. The band is closely applied to the nucleus as shown in *fig. 26*. The nuclear membrane is very weak in this region, and the nuclear structure indicates a movement of material toward the point of attachment. The connection between the nucleus and the band is maintained, even after the band has come to the surface (*fig. 28*). In the mature sperm the band is a spiral of five or six turns, the direction being, almost without exception, from left to right, as viewed from above. The radiations, which were so conspicuous during the growth of the blepharoplast, disappear as the blepharoplast breaks up into granules.

The two sperms are formed within the two cells resulting from the division of the body cell. That this is the case is readily seen in sections (*figs. 28, 29, 32*). The relations are particularly clear in *fig. 29,* in which *t* is the pollen tube, and *w* the wall of the sperm mother cell. The figure shows the apex of the sperm with a small portion of its large nucleus still surrounded by the mother cell. The two sperms within their mother cells are shown in the photomicrograph, *fig. 32*.

That the sperms are formed within mother cells is also clearly seen in living material, where the mother cells enlarge considerably after the sperms are ready to move. The peripheral portion of the partition between the two sperms breaks down, thus allowing the sperms to move about within the old body cell. At this stage the term body cell is not strictly correct, because the cavity now consists of the combined areas of the two sperm mother cells. Since, however, the outer wall is still the wall of the original body cell and there is no name for the new cavity, we may refer to it as the old body cell. The wall of the old body cell soon breaks down and the sperms escape into the main portion of the tube.

Sperms within the pollen tube measure about 200 μ in diameter and about 275 μ from apex to base. After leaving the tube, they increase somewhat in size, reaching a diameter of 230 μ and a length of 300 μ. Consequently, they are easily visible to the naked eye.

The living sperm, as seen under the microscope, has a large granular nucleus, surrounded by a thin and almost colorless sheath of cytoplasm, which is somewhat thicker at the spiral end. The nucleus usually shows a large depression just beneath the apex of the sperm (*fig. 32*).

The movements of the sperms are easily observed by simply mounting a piece of the nucellus with its pollen tubes. In addition to the lighting from above, some light may be reflected up through the pollen chamber. The upturned ends of the pollen tubes (*fig. 27*) are so transparent that they scarcely obscure the view. The cilia begin to move while the sperms are still fast together and more or less attached to the stalk cell. The movement of cilia is accompanied by pulsating and amoeboid movements which continue for an hour or more before the sperms separate. After the separation, they may swim for half an hour or more in the old body cell before they escape into the general cavity of the tube. Occasionally, the sperms are still attached to each other after they have escaped into the tube, and in such cases their movements are awkward, because they naturally try to move in opposite directions. When free from each other the principal movement is straight ahead, with a rotation on the long axis. The sperms swim up and down in the tube, going up as far as the diameter of the tube will permit, and then coming back. The amoeboid movements both of the cytoplasm and the nucleus are quite noticeable, especially while the sperm is changing its direction. At the apex, where the cytoplasmic sheath is thickest, the amoeboid movement is most conspicuous, and may be so rapid that it is more like a twitching. How long the sperms might swim in the pollen tubes under natural conditions, one could hardly guess. When a nucellus is inverted in a drop of sugar solution on a slide, and is still further protected by a bell jar, the movements have continued for five hours.

After the sperms begin to move, there is a rapid increase in the turgidity of the tube, which sooner or later ruptures at or near the exine of the pollen grain. Most of the starch and liquid contents of the tube escapes with a spurt, unless one of the sperms is immediately drawn into the opening. The first sperm may escape in two or three seconds, but the other may be half a minute in getting out, probably because there is not so much pressure behind it. The rupture is often not more than 50 μ in diameter, while the average sperm is four times as broad. But however much the sperm may be constricted in getting out, it promptly regains its form and begins to swim.

Efforts to keep the sperms alive after their escape from the pollen tube were not very successful. In weak sugar solutions they immediately break to pieces, almost explode. In a 10 per cent. sugar solution they quickly die. Sugar was added to a 10 per cent. solution until it became, perhaps, a 12 or 15 per cent. solution, and in this the sperms continued to swim for several minutes. No experiments were made to determine whether the sperms are chemotactic or not.

The material would have allowed a more detailed account of the later history of the blepharoplast and the development of the sperm, but these features, particularly the relation of the blepharoplast to the spiral band, are shown so much more clearly in my preparations of Ceratozamia, that I have refrained from any extended description at this time.

The further history of the sperm of *Dioon edule* will be considered in a forthcoming paper on fertilization and embryogeny.

DISCUSSION

With THIESSEN'S (14) paper on the seedling of *Dioon edule*, my own paper on the ovule and female gametophyte, the present paper on spermatogenesis, and a study of fertilization and embryogeny now nearly completed, considerable information concerning this form is available. The temptation to draw conclusions is strong, but studies on *Ceratozamia mexicana* and *Dioon spinulosum* are well under way, and Sister HELEN ANGELA (12) has already completed an investigation of the anatomy of Ceratozamia. Since any theories will be more likely to be well founded if based upon a comparative study, I shall reserve speculations for a safer opportunity. At present I shall merely consider a few points suggested by the foregoing description.

The largest staminate sporophylls in the Cycadales are found in Cycas and the smallest in Zamia. The number of sporangia corresponds, roughly, to the size of the sporophyll. The sporangia in Cycas, Encephalartos, Dioon, and all the forms with large microsporophylls, so far as I have been able to examine them, have the sporangia in definite sori with 3, 4, or 5 sporangia in a sorus. In forms with smaller sporophylls, like Zamia, Ceratozamia, and Microcycas, some of the sporangia are single, but most of them are grouped, with 2 or 3, or occasionally 4 sporangia in a sorus. CALDWELL (9) states that in Microcycas the sporangia are not arranged in sori, but his photograph shows that even on the smaller sporophyll most of the sporangia are in sori; the number of sporangia is about 100 on the larger sporophyll. The number of sporangia on a sporophyll, according to Miss GRACE SMITH (8) is as follows: *Cycas circinalis* 700, *Encephalartos Caffer* 700, *Macrozamia Miquelii* 600, *Encephalartos villosus* 500, *Dioon edule* 200, and *Zamia floridana* 24. We can now add that the number in *Dioon edule* often reaches 300, the usual number in *Ceratozamia mexicana* is 250 to 300, and in *Stangeria paradoxa*, about 260. In both Ceratozamia and Stangeria the sporangia are very small.

If this is a reduction series, as we believe it is, Microcycas, so far as this character is concerned, has scant claim to the position of "the most primitive cycad yet described," especially since LAND (**10**) from a consideration of the female gametophyte, and Sister HELEN ANGELA (**13**) from an investigation of the vascular anatomy, have concluded that Microcycas is far from primitive. As far as microsporophylls and microsporangia are concerned, Dioon is nearer the Cycas condition than any other western cycad.

The output of spores is very easily estimated. BOWER'S studies on spore-producing members have shown that the more primitive ferns have a large output, which is gradually reduced as we pass to the highly specialized recent forms. We believe the same is true of cycads. The output in *Dioon edule* is about 30,000 spores per sporangium. According to Miss GRACE SMITH (**8**) the output in *Encephalartos villosus* is 26,000, in *Ceratozamia mexicana* 8000, and in *Zamia floridana* 500 to 600. It would be interesting to know the output in the other cycads. I should expect an output of 30,000 or more in Cycas, and should be surprised if the output in Microcycas reached 20,000. Judging from CALDWELL'S (**9**) account, I should look for an output of about 10,000 spores.

In our study of the spore coats, I looked for the third coat described by FERGUSON (**4**). The fact that only an intine and an exine are present in Dioon led me to reexamine *Pinus Laricio*. I found only an exine and an intine, as in Dioon, the third coat described by Miss FERGUSON (**4**) being merely the usual intine which her excellent technic had sharply differentiated from the exine. As preparations show and her own figures indicate, the intine, which she mistakes for a third coat, grows out to form the pollen tube.

The blepharoplast in *Dioon edule* is probably of nuclear origin. IKENO (**1**) was inclined to believe that the blepharoplasts of *Cycas revoluta* came from the nucleus, although when first recognizable they are small bodies just outside the nuclear membrane. WEBBER (**2**) finds that in Zamia the blepharoplasts originate *de novo* in the cytoplasm of the body cell, but no convincing early stages are given. CALDWELL'S (9) material was all too far advanced to show the origin of the blepharoplasts.

It seems probable that the manner in which the spiral band is formed from the blepharoplast is similar, in its main features, in all the cycads. The solid blepharoplast becomes vacuolated and then breaks up into a group of granules from which the ciliated band is formed. CALDWELL (9) describes in Microcycas a band, already distinct during the division of the body cell, and says that this band becomes broken up into fragments upon which the beginnings of cilia may be seen. His *fig. 25* indicates that the band is a section of the rim of the much vacuolated blepharoplast, while the "fragments" in his *fig. 27* are sections of the spiral band, which has already made several turns. The cilia which he figures on the inside of the fragments need confirmation.

The origin of the blepharoplast in pteridophytes has been considered by several investigators, all of whom agree that it first appears in the cytoplasm. Some find it present even from the early spermatogenous divisions, while others find it first in the cell which is to give rise to two sperm mother cells, or, occasionally, one generation earlier than this. In a very detailed account of spermatogenesis in Nephrodium, YAMANOUCHI (11) finds that two blepharoplasts first appear in the cell which is to give rise to two sperm mother cells. The blepharoplast in pteridophytes simply elongates and forms the band directly, there being no radiations, no vacuolation, nor breaking-up into a group of granules which subsequently give rise to a spiral band. While the blepharoplasts of ferns and cycads are doubtless homologous structures, no intermediate conditions have yet been found which would explain the behavior of the blepharoplasts of cycads.

In *Dioon edule*, as in nearly all gymnosperms, only two sperms are formed in the pollen tube. In a few instances I have noted four sperms in the pollen tube of *Ceratozamia mexicana*. JUEL (3) found four to twenty sperms in the pollen tube of *Cupressus Goweniana*, and naturally regarded the condition as primitive. CALDWELL (9) found sixteen or twenty sperms in *Microcycas calocoma*, and on the basis of this character claimed Microcycas to be the most primitive cycad yet described.

That the two sperms represent a reduction from a larger number is so evident that there is no need for discussion, but a word in regard to the so-called "body cell" from which they are produced may not be out of place. In the cycads, in Ginkgo, and in Coniferales the cell whose division gives rise to the "stalk cell" and body cell is often called the generative cell, probably because the stalk cell is regarded as a spermatogenous cell which has ceased to function. In Cupressus, Microcycas, and Ceratozamia all the sperms come from the body cell, the stalk cell being entirely sterile. It might be suggested that the stalk cell corresponds to the basal cell of the ordinary fern antheridium and that the dome cell corresponds to the pollen tube, while the primary spermatogenous cell corresponds to the body cell. If the dome cell, without forming the usual cover cell, should become elongated, we should have very much the same situation as that found in *Cupressus Goweniana*, *Microcycas calocoma*, and *Ceratozamia mexicana*. The diagram (*fig. 33*) indicates these homologies in an ordinary polypod fern and a cycad. The fact that in the fern the dome cell is sister to the spermatogenous cell, while in the cycad the stalk and spermatogenous cells are sisters, might be

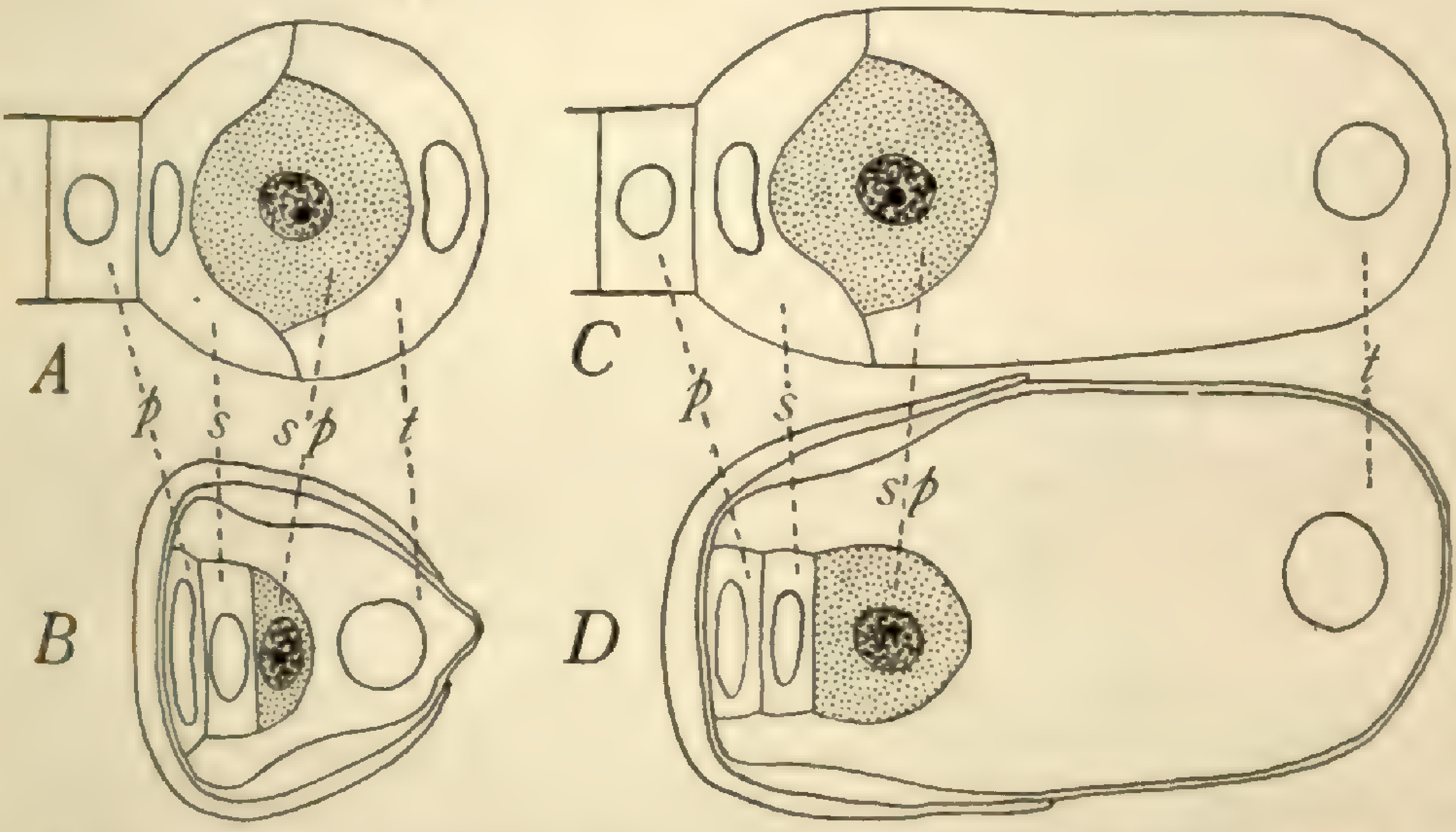

FIG. 33.—Diagram illustrating the homologies between the parts of an ordinary polypod fern antheridium and the pollen tube structures of a cycad: *A* and *C*, the fern antheridium, in *C* the dome cell being represented as elongated into a tube; *B* and *D* the cycad structures: *p*, prothallial cell; *s*, stalk cell; *sp*, spermatogenous cell; *t*, tube cell.

regarded as an objection by those who lay great stress upon the importance of a rigid sequence of cell divisions.

I have shown that in *Dioon edule* the sperms are formed within sperm mother cells from which they are subsequently discharged. IKENO (**1**) does not state whether the sperms of Cycas are formed within mother cells or not. WEBBER (**2**) claims that in Zamia they are not formed within mother cells, but that the two cells resulting from the division of the body cell become ciliated. CALDWELL (**9**) does not mention this feature in his account of Microcycas and his figures are noncommittal. MIYAKE (**6**) saw the sperms within the body cell in Ginkgo, but could not make a definite statement for Cycas. I have examined Zamia and find that the sperms are organized within definite sperm mother cells, and have found the same situation in Ceratozamia. This condition is probably general in cycads.

In bryophytes the final division of the spermatogenous cells results in conspicuous pairs of sperm mother cells, or perhaps, as has been claimed, two sperms are formed in a single mother cell. In pteridophytes the pairs are not so conspicuous, but the feature is just as definitely present. In nearly all gymnosperms the spermatogenous tissue has become reduced to a single pair of spermatogenous cells, which in some cases, as in Juniperus, bear a striking resemblance to the sperm mother cells of cycads. In Juniperus, however, no vestige of a blepharoplast has been reported, and it is assumed that the mother cells function directly as sperms. In forms like Pinus, there is merely a nuclear division within the body cell, giving rise to two sperm nuclei, no sperm mother cells being formed. In Pinus there are structures which may be vestiges of blepharoplasts. It would be interesting to know whether a cytological study of some form like Juniperus or Thuja would show non-ciliated sperms with vestiges of blepharoplasts within mother cells.

Enough is now known of the sperms of the four genera of occidental cycads to identify the genera by this character alone. A comparative study will be made later, but a few features will be mentioned here. In Cycas the spiral makes five and a half to six turns, the direction being from right to left, as viewed from above. In Zamia, according to WEBBER (**2**), there are five to six turns, always from left to right.

In Dioon also, the direction is from left to right. In Microcycas CALDWELL (9) figures three cases, one from right to left, and the direction of the other two uncertain. What causes the direction of spiral is not known.

Zamia has the largest sperm yet described, measuring 222 to 306 μ in diameter and 222 to 332 μ in length. In Cycas the diameter is 180 to 210 μ. In *Dioon edule* the living sperms measure about 230 μ in diameter and 300 μ in length. In microtome sections, the sperms are smaller, perhaps on account of plasmolysis, but more probably because the sperms increase in size after leaving the tube. In section the sperms measure about 200 μ in diameter and 275 μ in length. CALDWELL (9) gives no measurements, but, judging from his figures, the sperms are comparatively small, with a diameter of about 60 μ.

In all the cycads which have been studied, the movements of the sperms are very similar, a forward movement with a rotation upon the long axis. While experiments have been made, no chemotaxis has yet been noted. When the sperms are mature, the neck canal cells are very large and turgid. It may be that they exert a chemotactic influence.

If the foregoing account seems to consist rather largely of data, I can only say that I prefer to reserve any discussion of phylogeny until the investigations in which I am already engaged shall have been completed.

SUMMARY

The sporophylls of the staminate cone are rather large, and bear about 250 sporangia, a larger number than in any cycads except Cycas, Encephalartos, and Macrozamia. The output of spores per sporangium is about 30,000, a larger output than in Zamia, Ceratozamia, or Encephalartos, the only genera in which this feature has been noted.

There are twelve chromosomes in the pollen mother cell, but they often split so early that the number may appear larger.

There is only one prothallial cell and that is persistent. The report of an evanescent prothallial cell in Zamia is probably due to a misinterpretation.

The blepharoplasts are very probably of nuclear origin. The radiations are streams of cytoplasm, which, in early stages, have a peculiar appearance on account of the granules and globules which adhere to them. The solid blepharoplast becomes vacuolated and then breaks up into granules from which the spiral band is formed. The ciliated band makes five or six turns from left to right. The sperms are larger than those of Cycas or Microcycas, but not quite so large as those of Zamia.

The sperms are formed within sperm mother cells, from which they are discharged. The same is true of Zamia, Ceratozamia, and probably of other cycads.

In addition to the movement by cilia, there is a vigorous amoeboid movement of both nucleus and cytoplasm.

Discussion of phylogeny will be reserved until investigations now in progress have been completed.

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EXPLANATION OF PLATES XV–XVIII

Figs. 1, 2.—In text.

PLATE XV

Fig. 3.—Transverse section of a young microsporophyll, showing sori, *s*, mucilage ducts, *m*, and vascular bundles, *b*. ×10.

Fig. 4.—Two microsporangia of sorus. ×55.

Fig. 5.—Section of a part of the microsporangium, showing epidermis, wall layers, tapetum, and some sporogenous tissue. ×250.

Fig. 6.—Microspore, Aug. 14, 1905. ×1260.

Fig. 7.—Microspore showing the prothallial cell, *p*, generative cell, *g*, and tube cell, *t*. ×1260.

Fig. 8.—The pollen tube is beginning to form. ×1260.

Fig. 9.—Pollen tube somewhat later. Oct. 1, 1907. ×1260.

Fig. 10.—The generative cell has divided to form the stalk cell, *s*, and body cell, *b*. Oct. 21, 1907. ×1000.

Fig. 11.—A later stage; black granules and gray bodies in the cytoplasm of the body cell. ×1000.

Fig. 12.—Nearly the same stage as *fig. 11*. ×1000.

Fig. 13.—Body cell showing black granules. Oct. 23, 1907. ×1890.

Fig. 14.—Body cell with black granules and gray bodies. Oct. 23, 1907. ×1890.

Fig. 15.—Beginning of radiations about the blepharoplasts. Oct. 30, 1907. ×945.

Fig. 16.—The blepharoplasts and radiations of the previous figures. ×1890.

PLATE XVI

Fig. 17.—Blepharoplast with radiations and gray bodies, *gb;* the figure shows the alveolar structure of the cytoplasm. ×1890.

Fig. 18.—Pollen tube structures with gray bodies on the radiations surrounding the blepharoplasts. Nov. 20, 1906. ×630.

Fig. 19.—General view of nucellus at stage shown in *fig. 18*, with pollen tubes and pollen chamber. ×30.

Fig. 20.—Blepharoplast with gray bodies on the radiations. Nov. 27, 1907. ×1890.

Fig. 21.—Later stage of blepharoplast and radiations. ×1890.

Fig. 22.—Still later stage. ×945.

Fig. 23.—View of nucellus just before the division of the body cell; the pollen chamber has extended entirely through the nucellus. ×8

PLATE XVII

FIG. 24.—Body cell with two blepharoplasts. ×945.

FIG. 25.—Pollen tube structures after the transverse orientation of the blepharoplasts. May 5, 1906. ×237.

FIG. 26.—Beginning of the spiral band. ×1890.

FIG. 26*a*.—Topography of pollen tube structures at the stage shown in *fig. 26*.

FIG. 27.—View of nucellus with pollen tubes at the stages shown in *figs. 26–29*. ×8.

FIG. 28.—Connection of the nucleus with the spiral band. ×945.

FIG. 29.—Apex of a sperm, showing that the sperm is organized within a mother cell: *t*, pollen tube; *w*, wall of sperm mother cell. ×800.

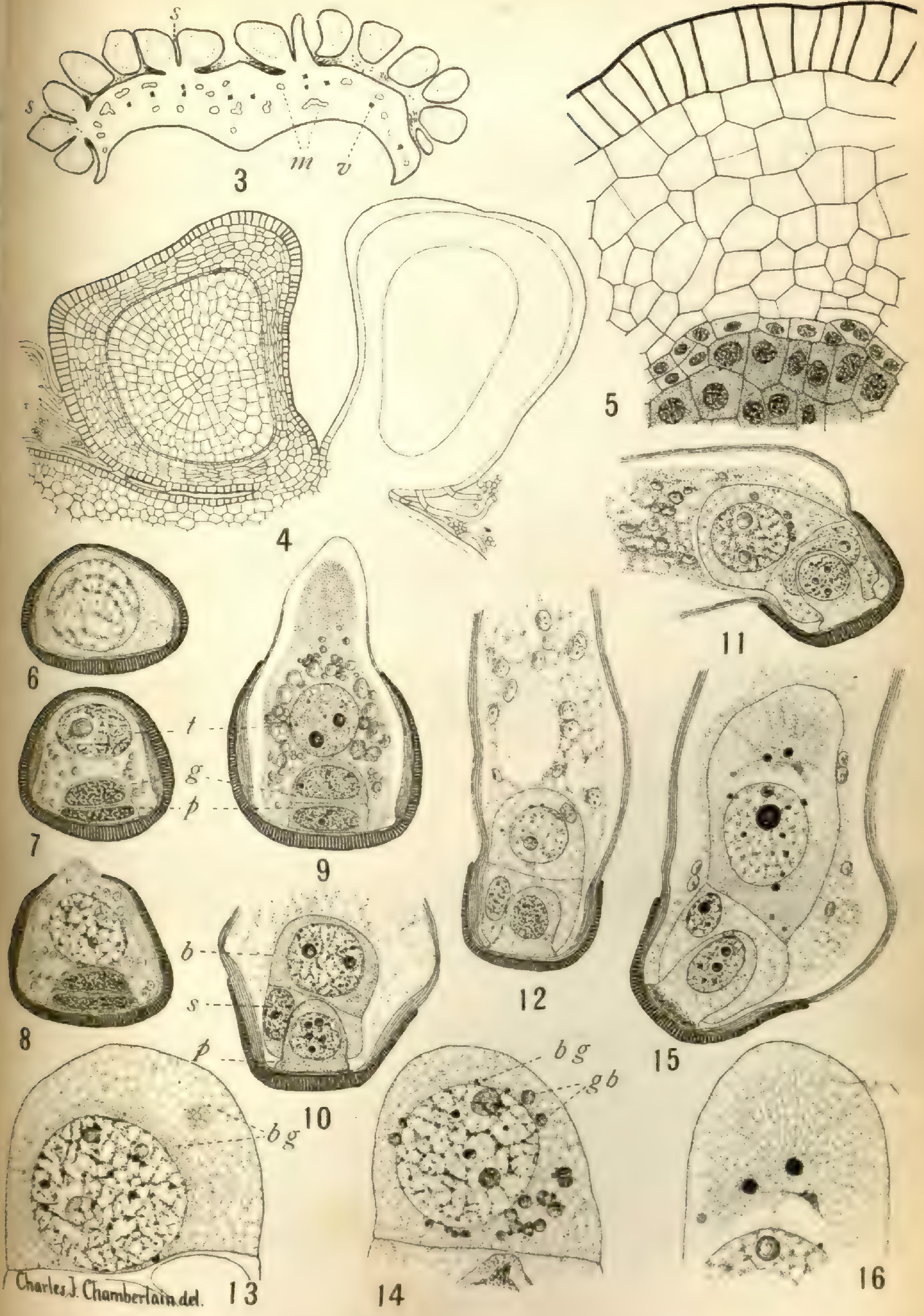
FIG. 30.—Transverse section of spiral band. ×945.

PLATE XVIII

FIG. 31.—Photomicrograph of pollen tube showing blepharoplast with gray bodies on the radiations. ×800.

FIG. 32.—Photomicrograph showing that the sperms are formed within mother cells. ×800.

FIG. 33.—In text.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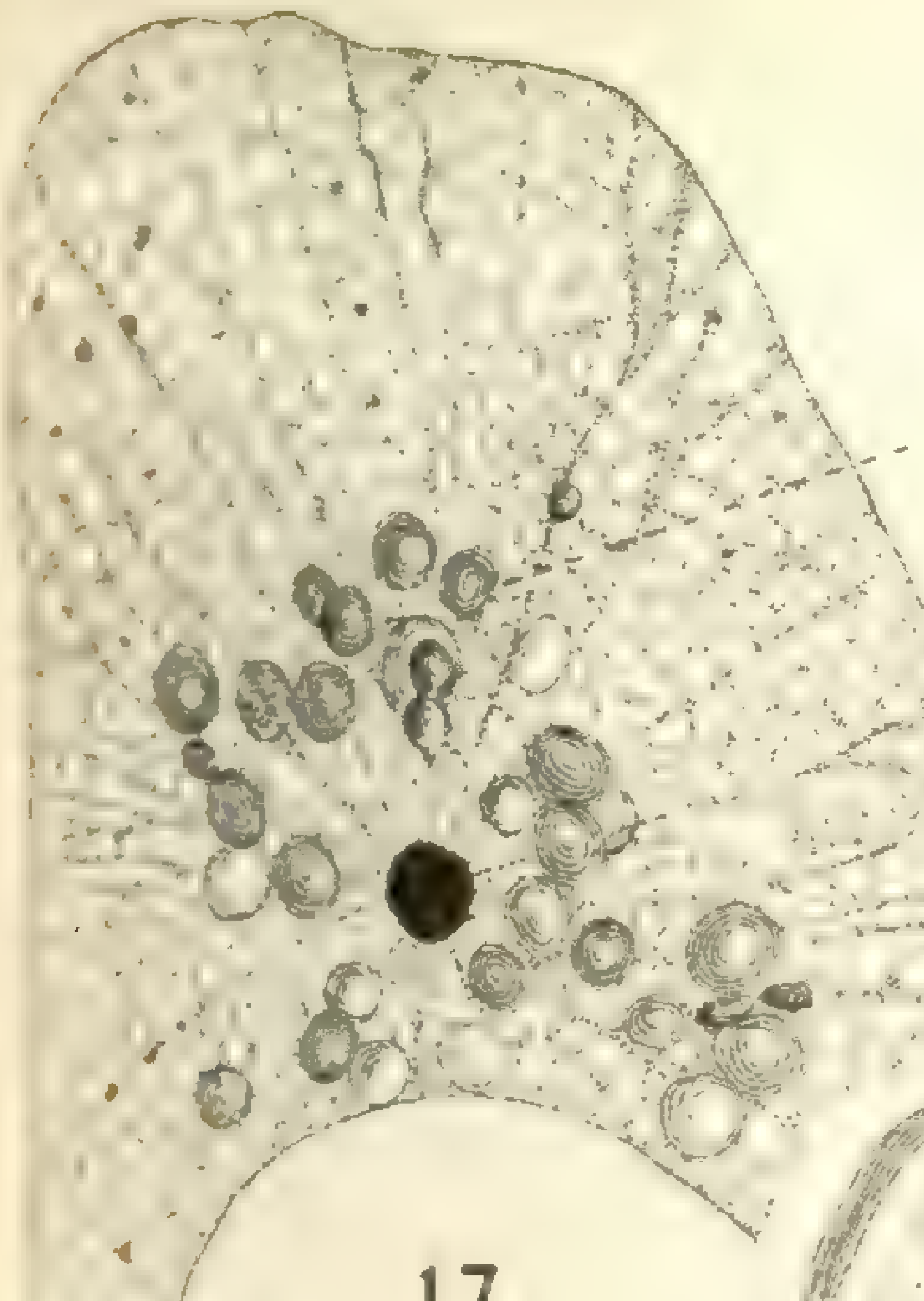
CHAMBERLAIN on DIOON



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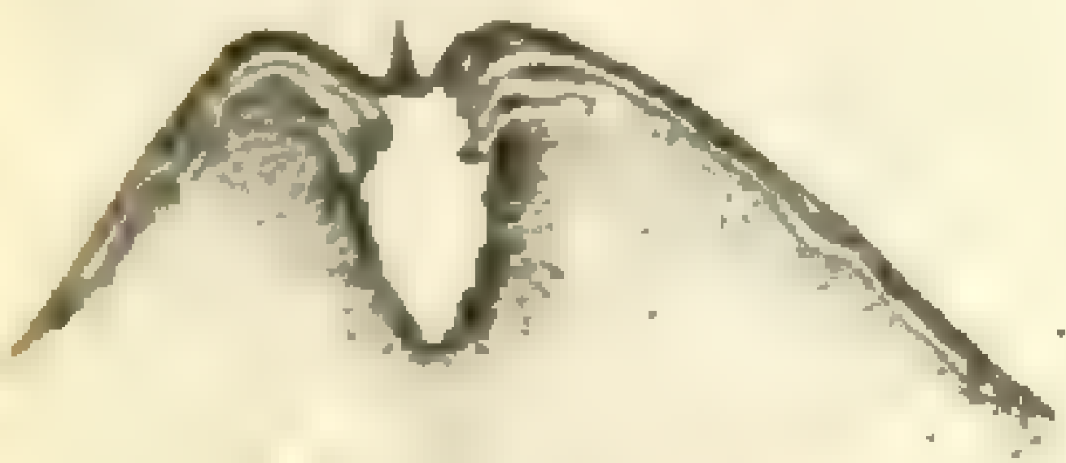

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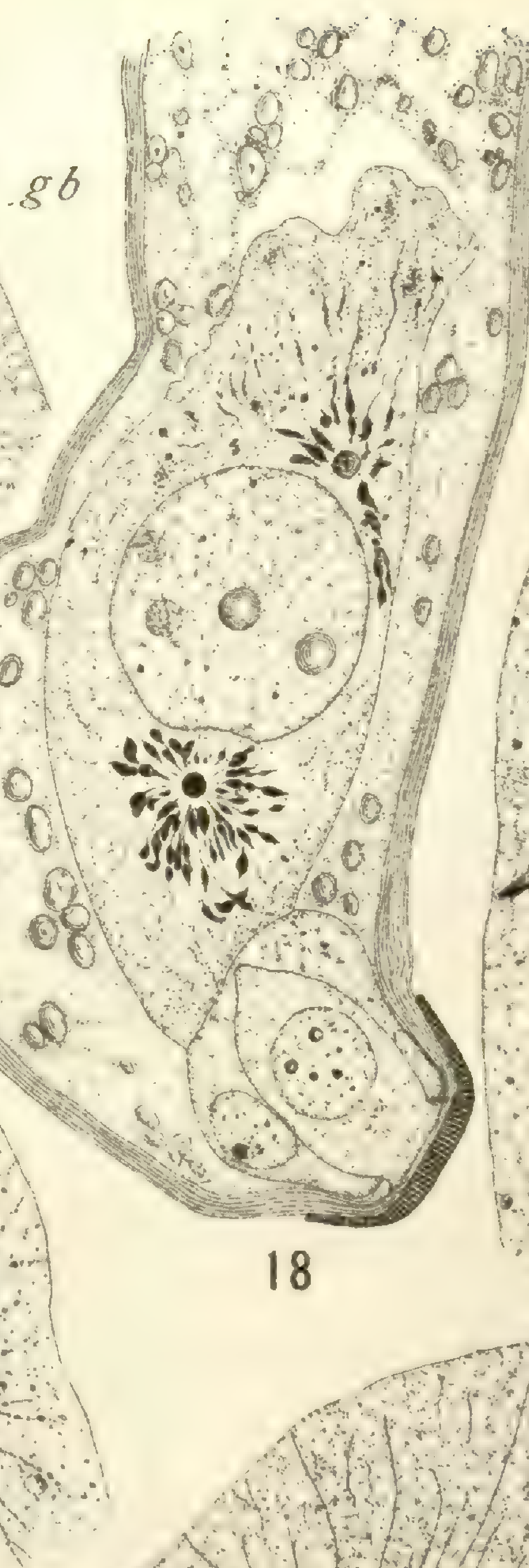

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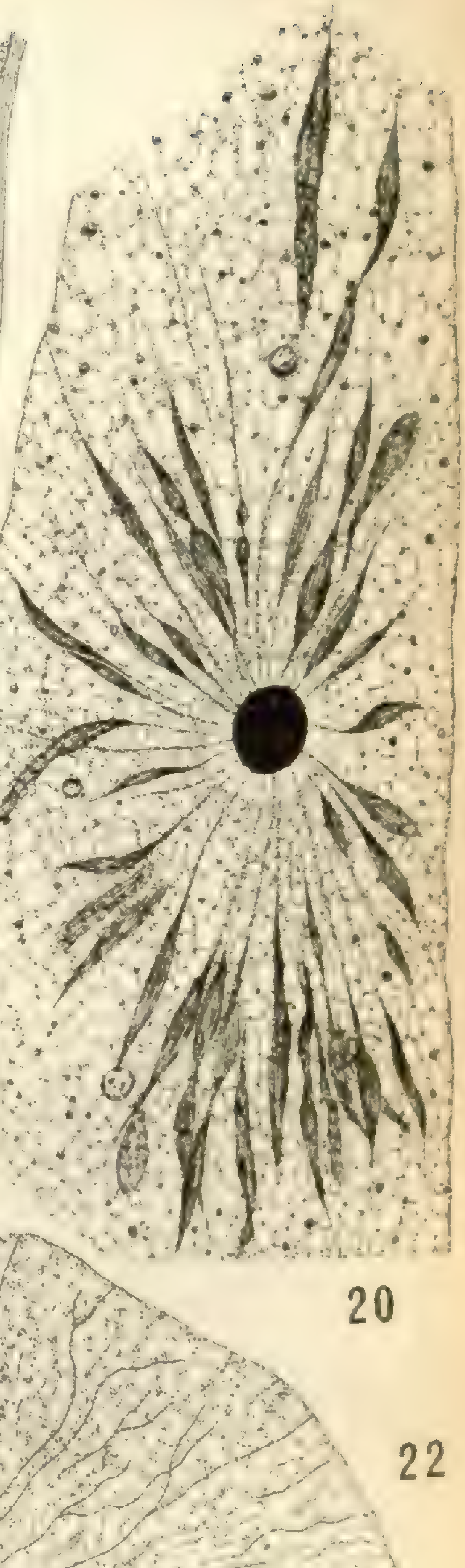

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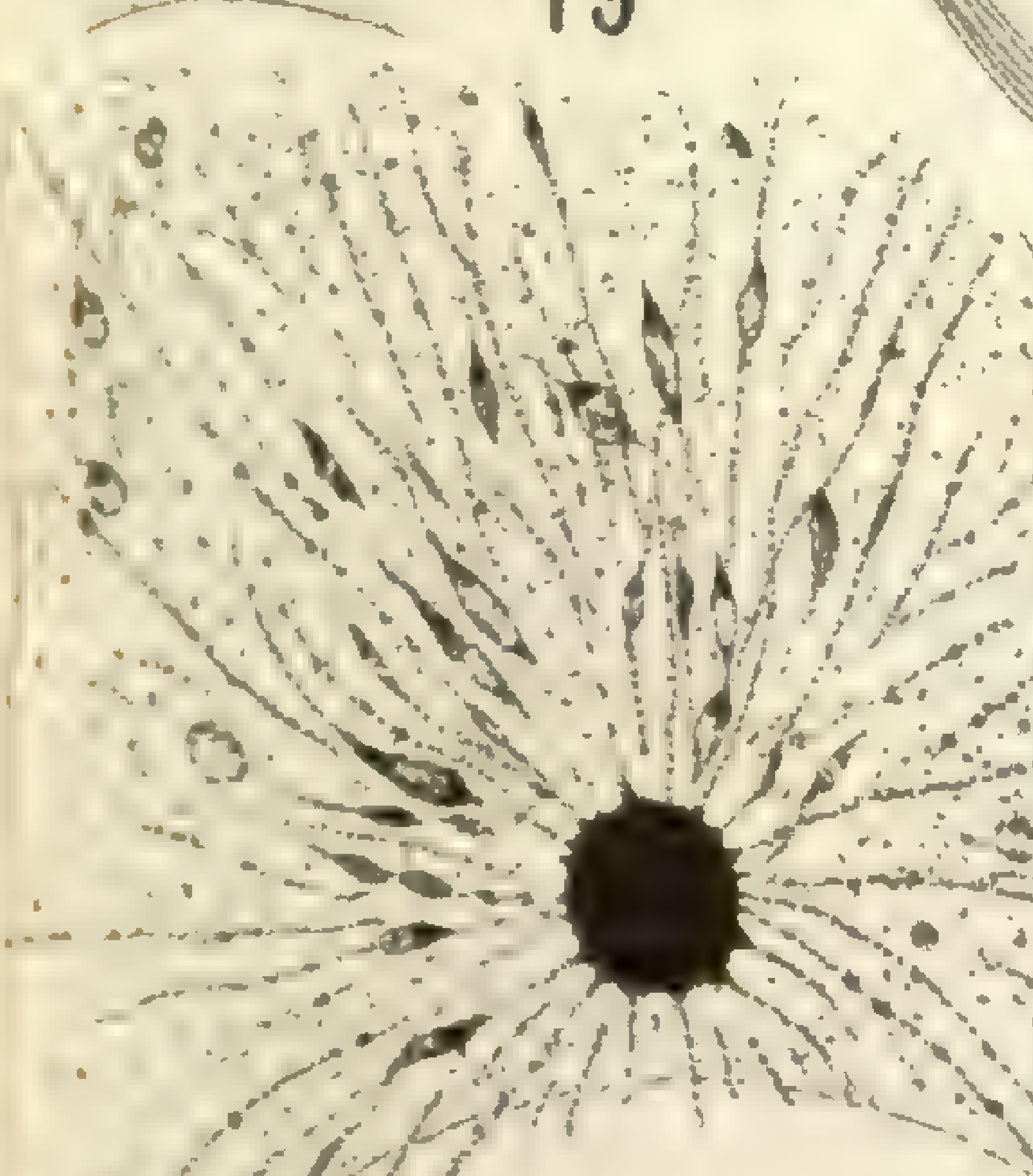

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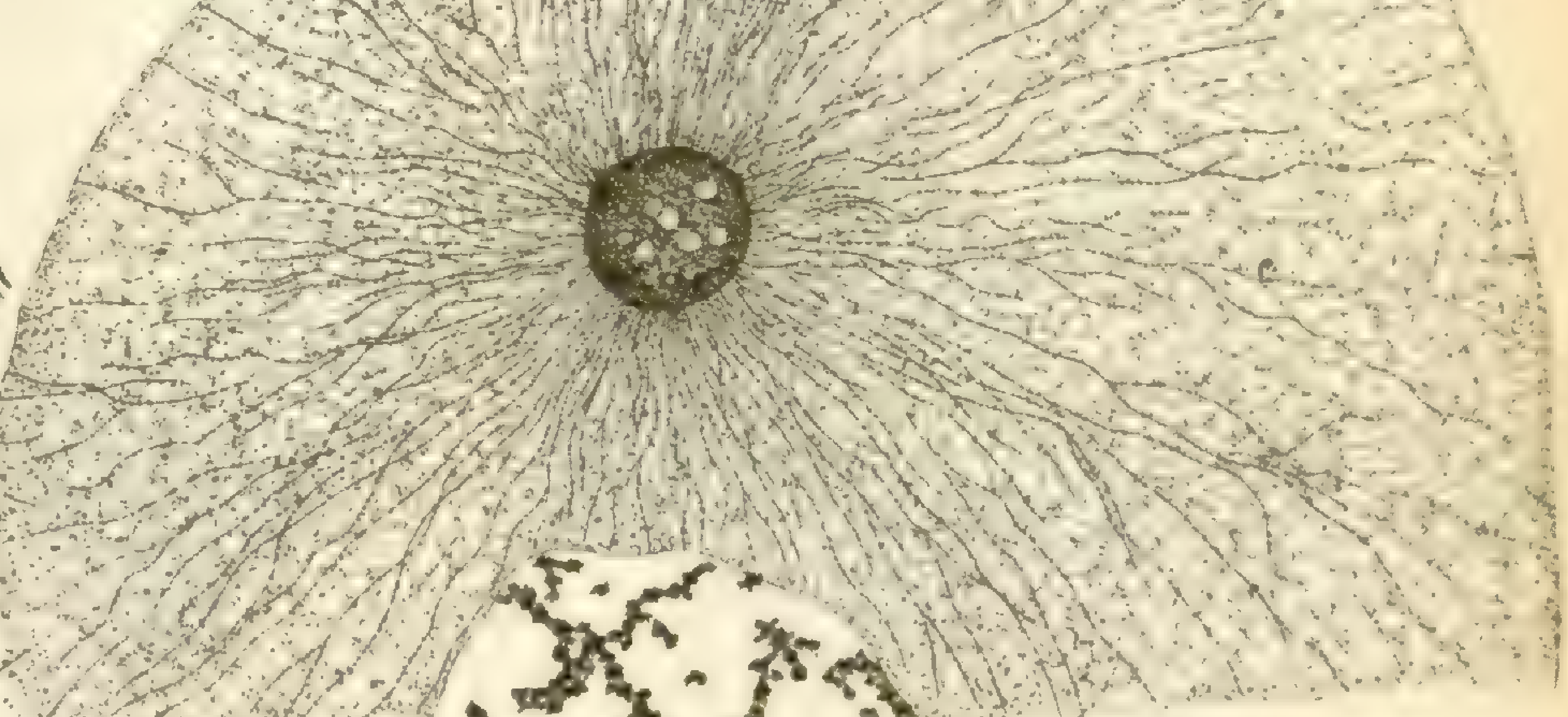

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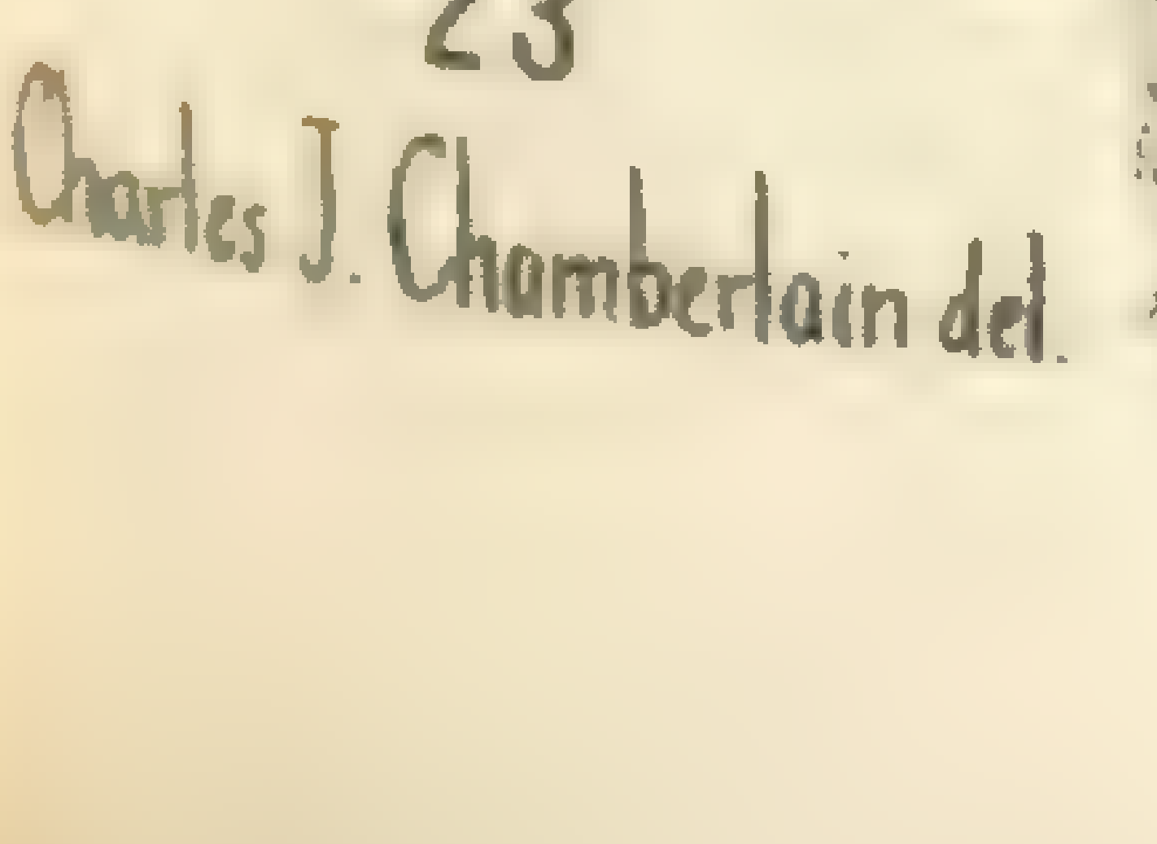

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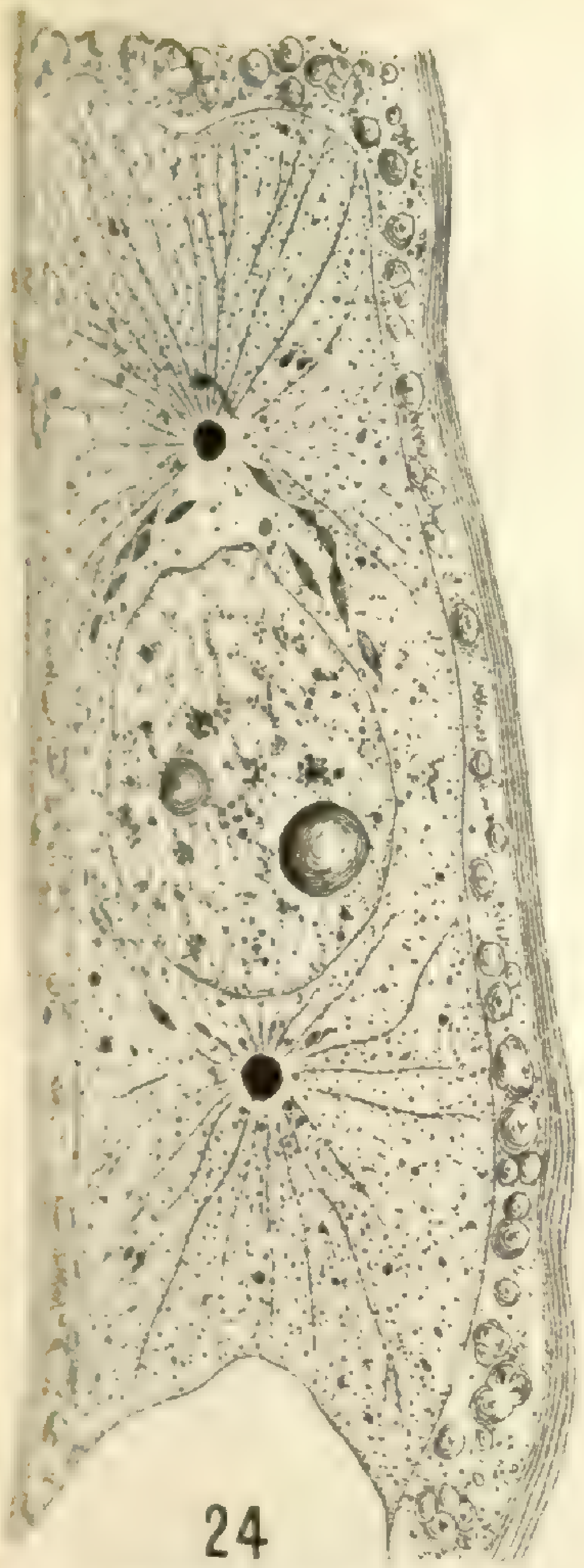

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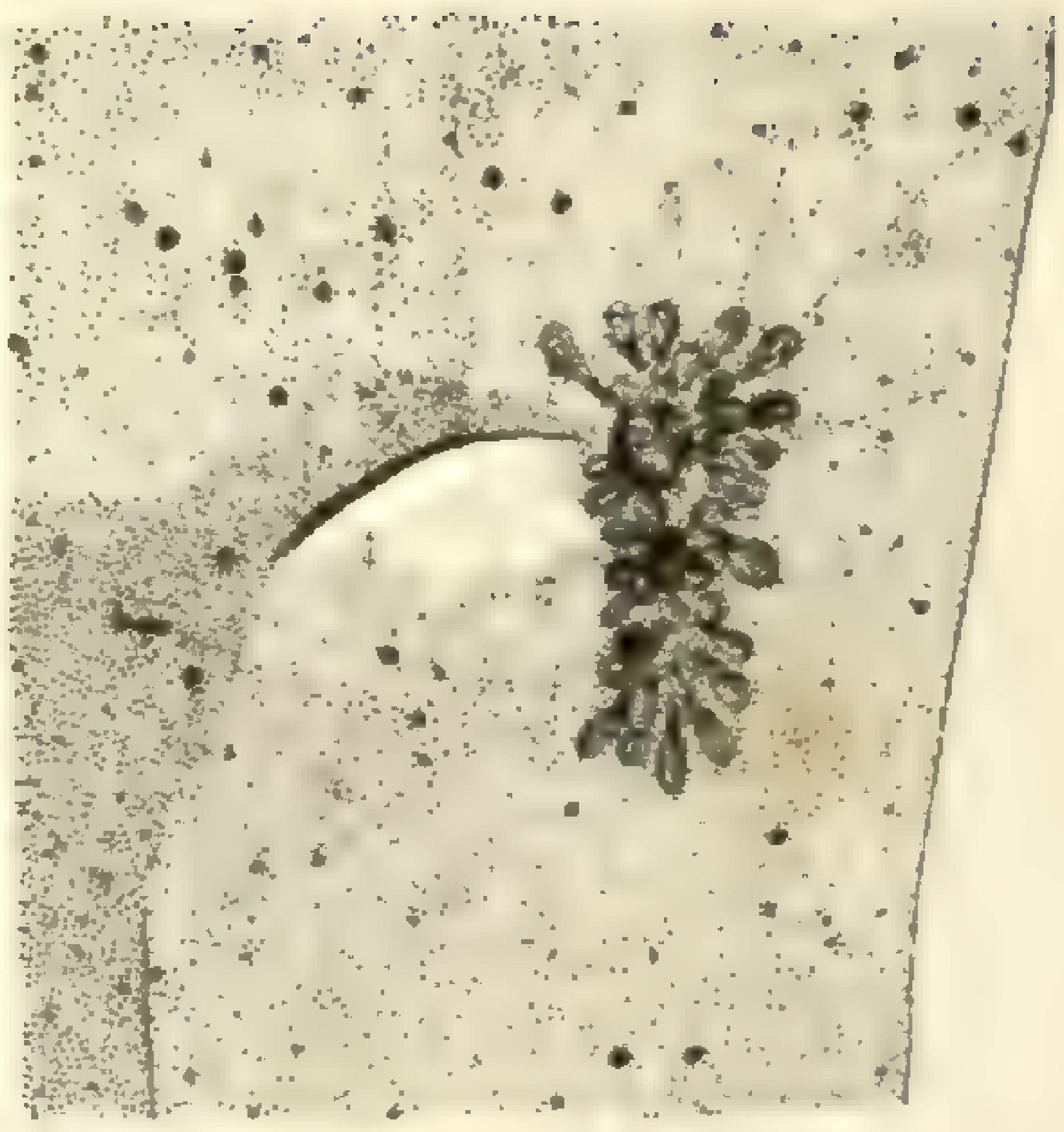

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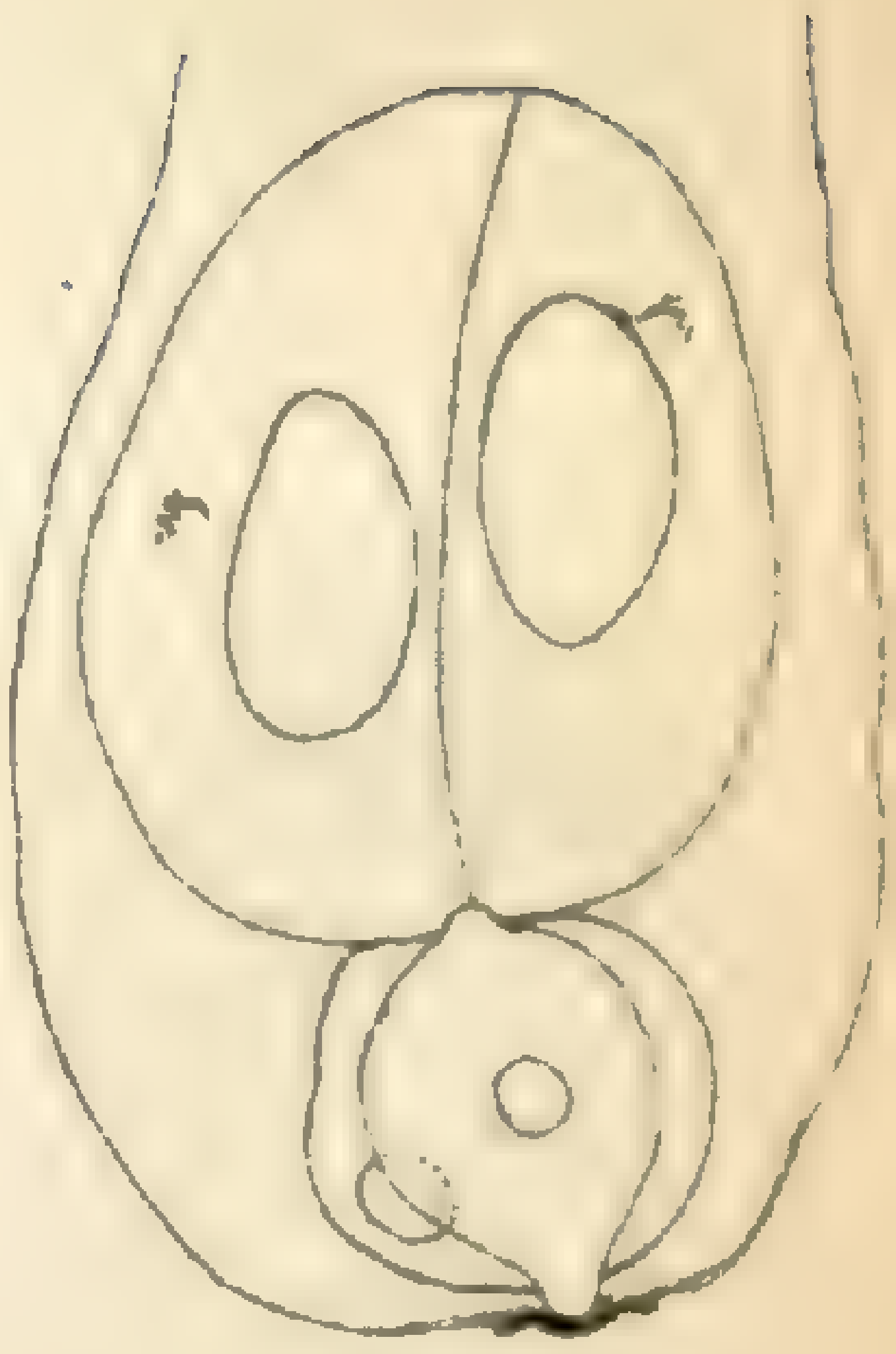

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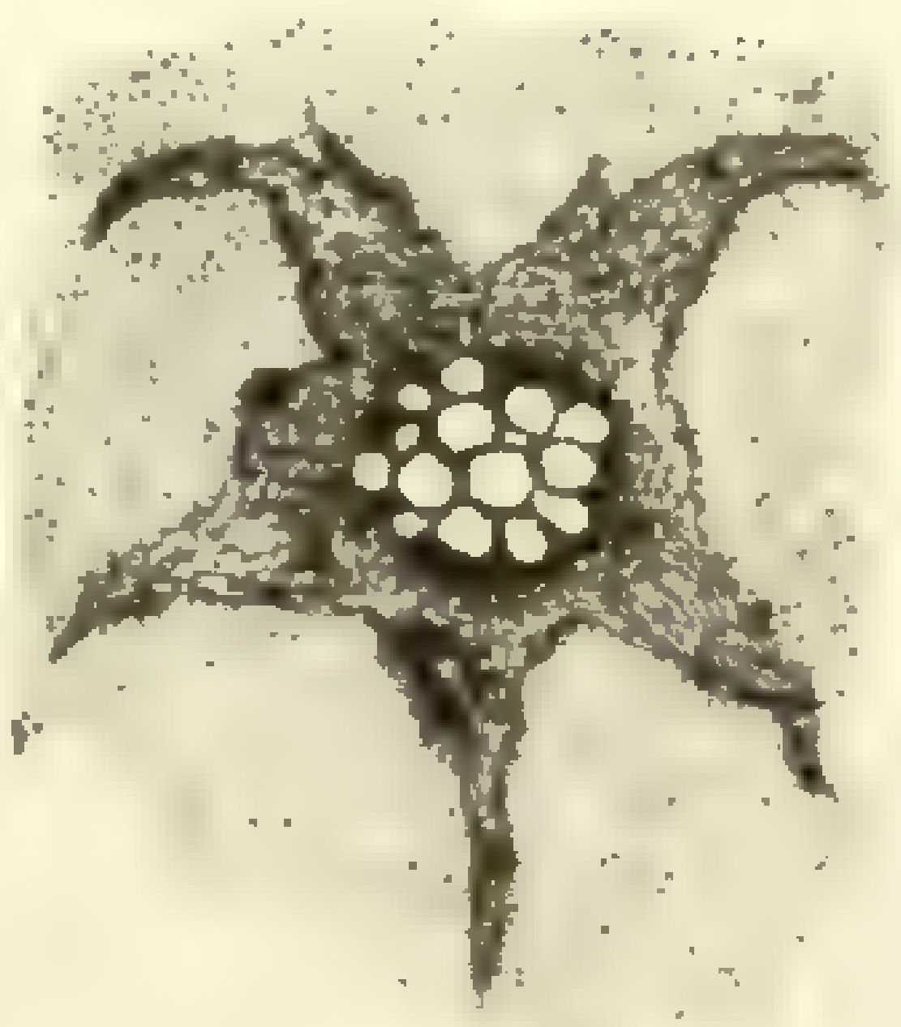

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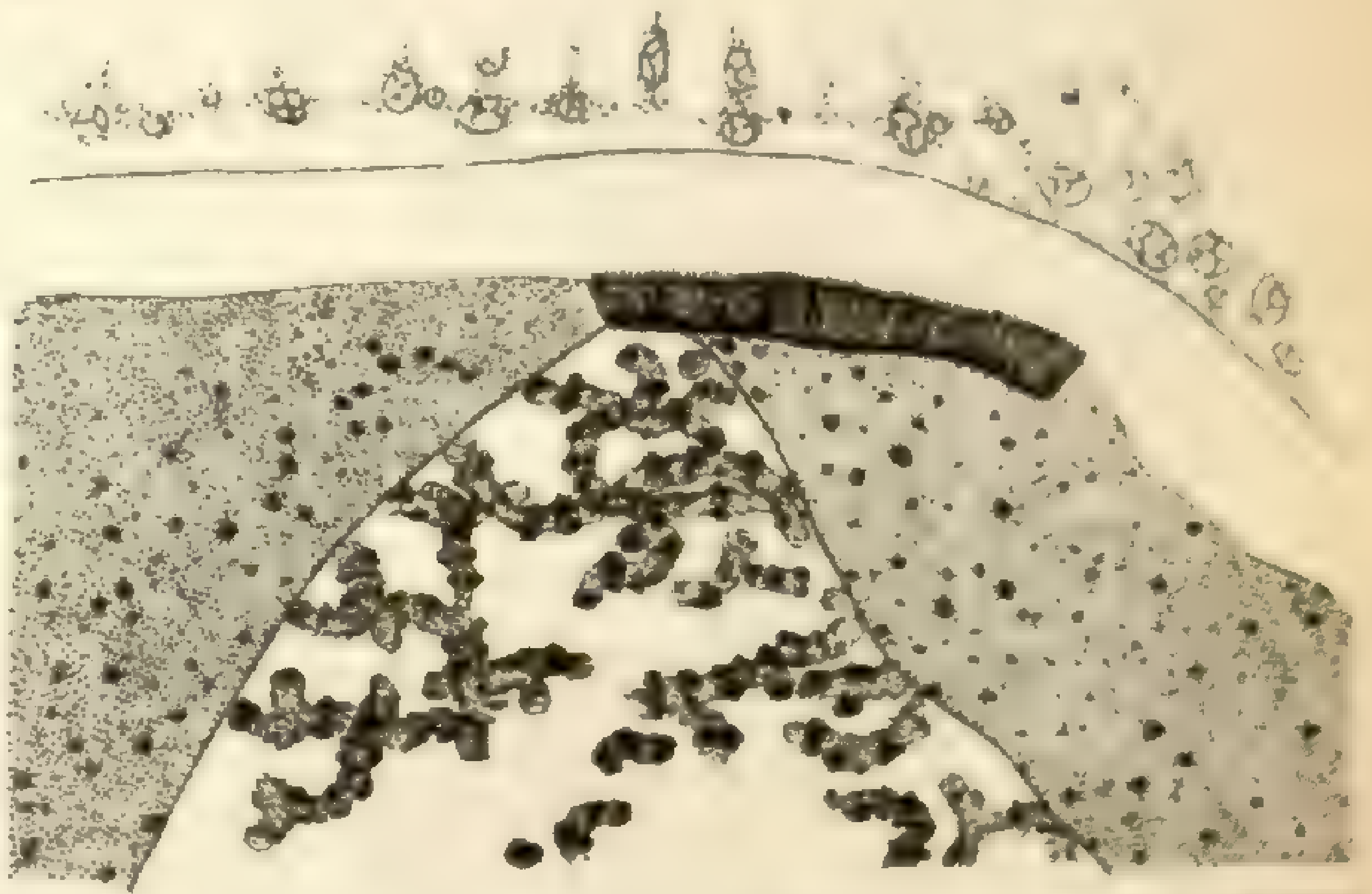

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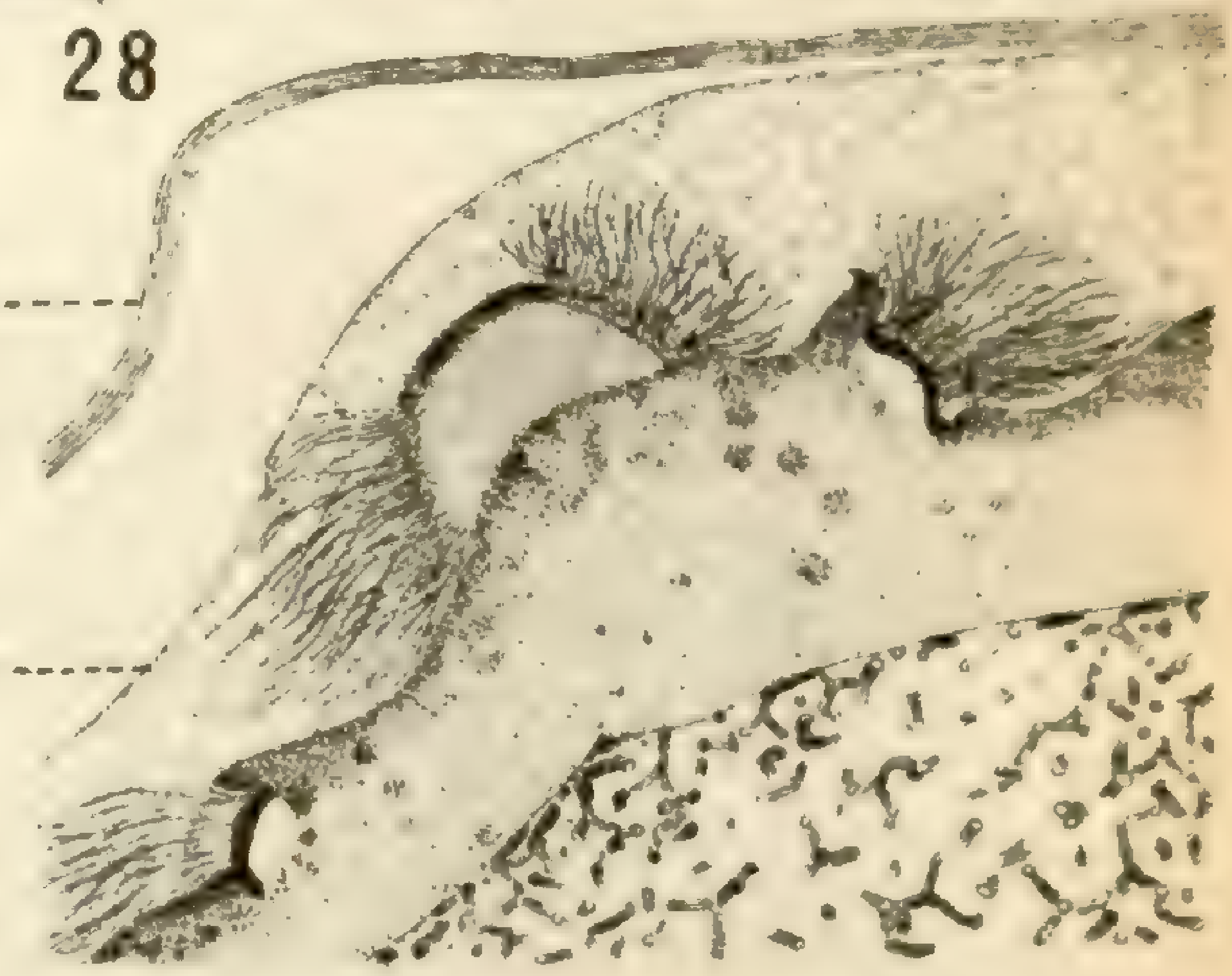

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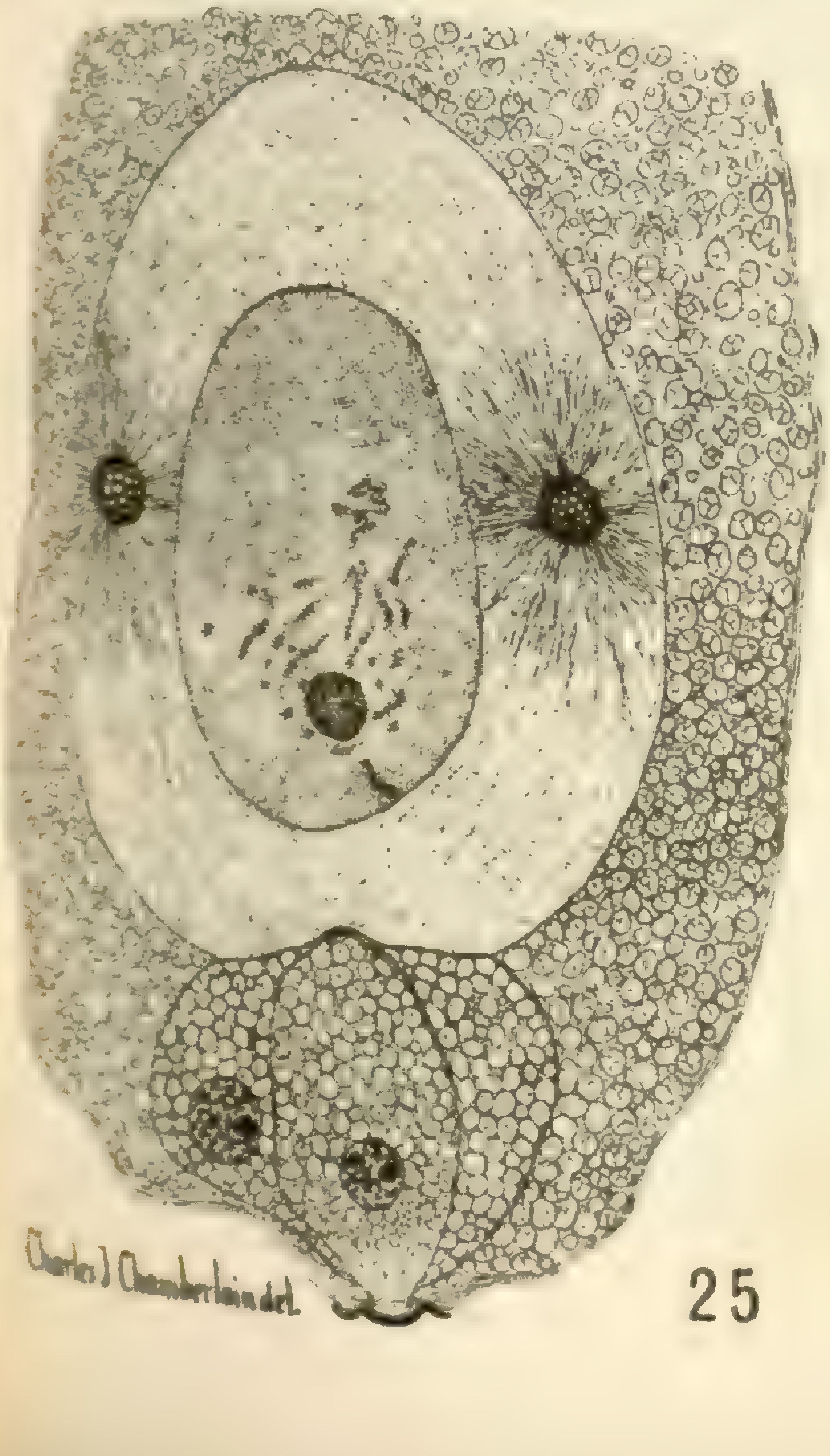

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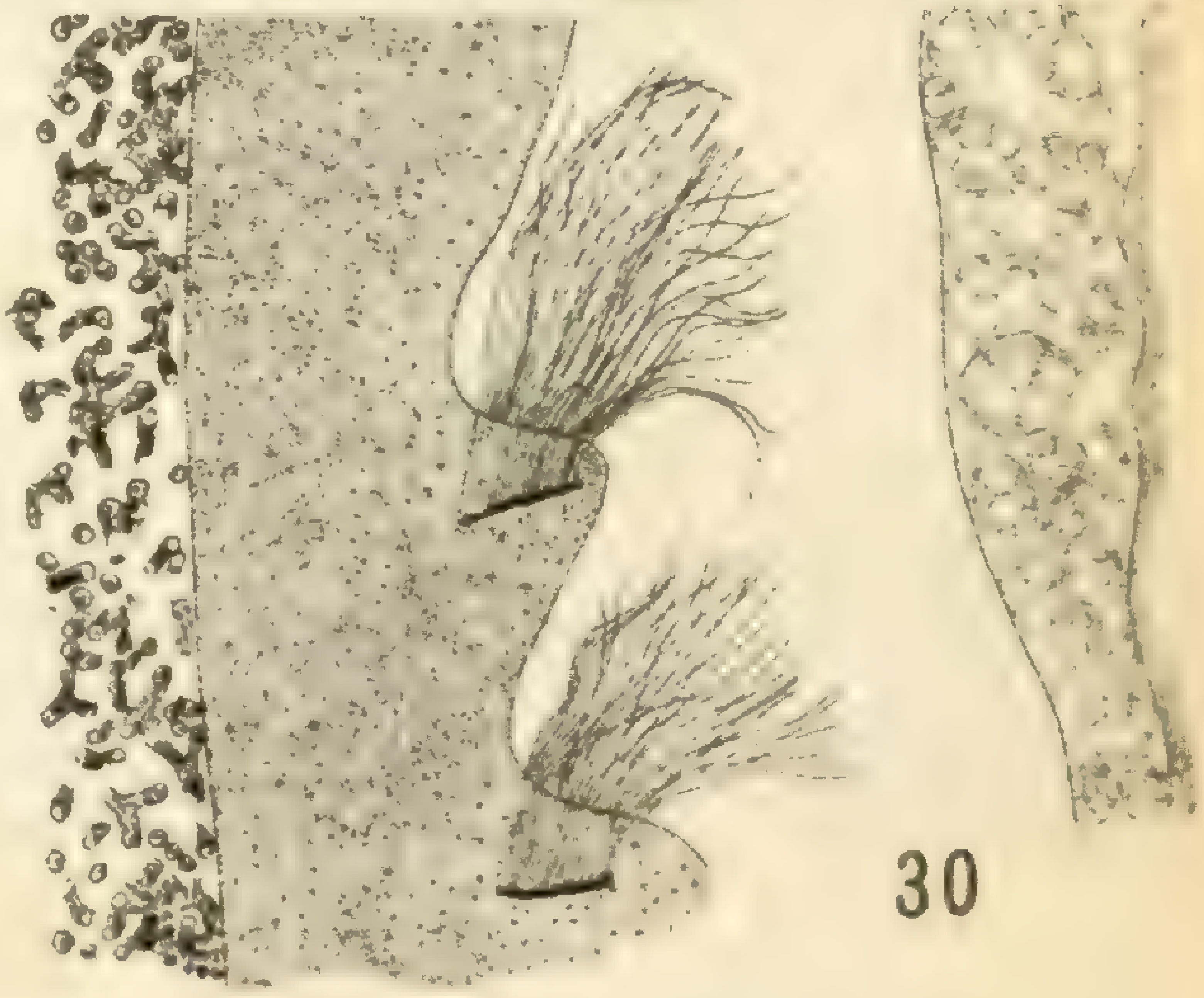

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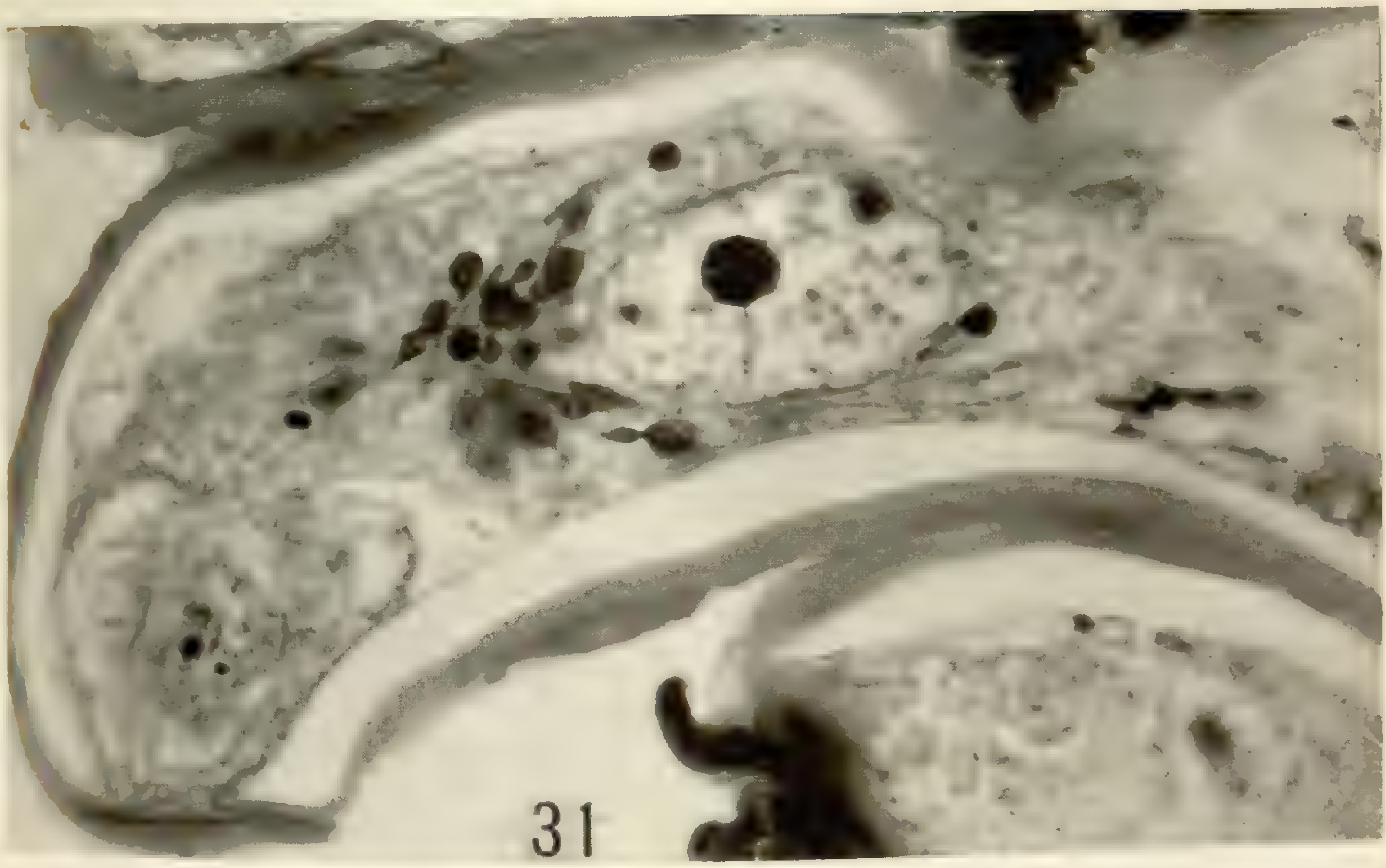
CHAMBERLAIN on DIOON



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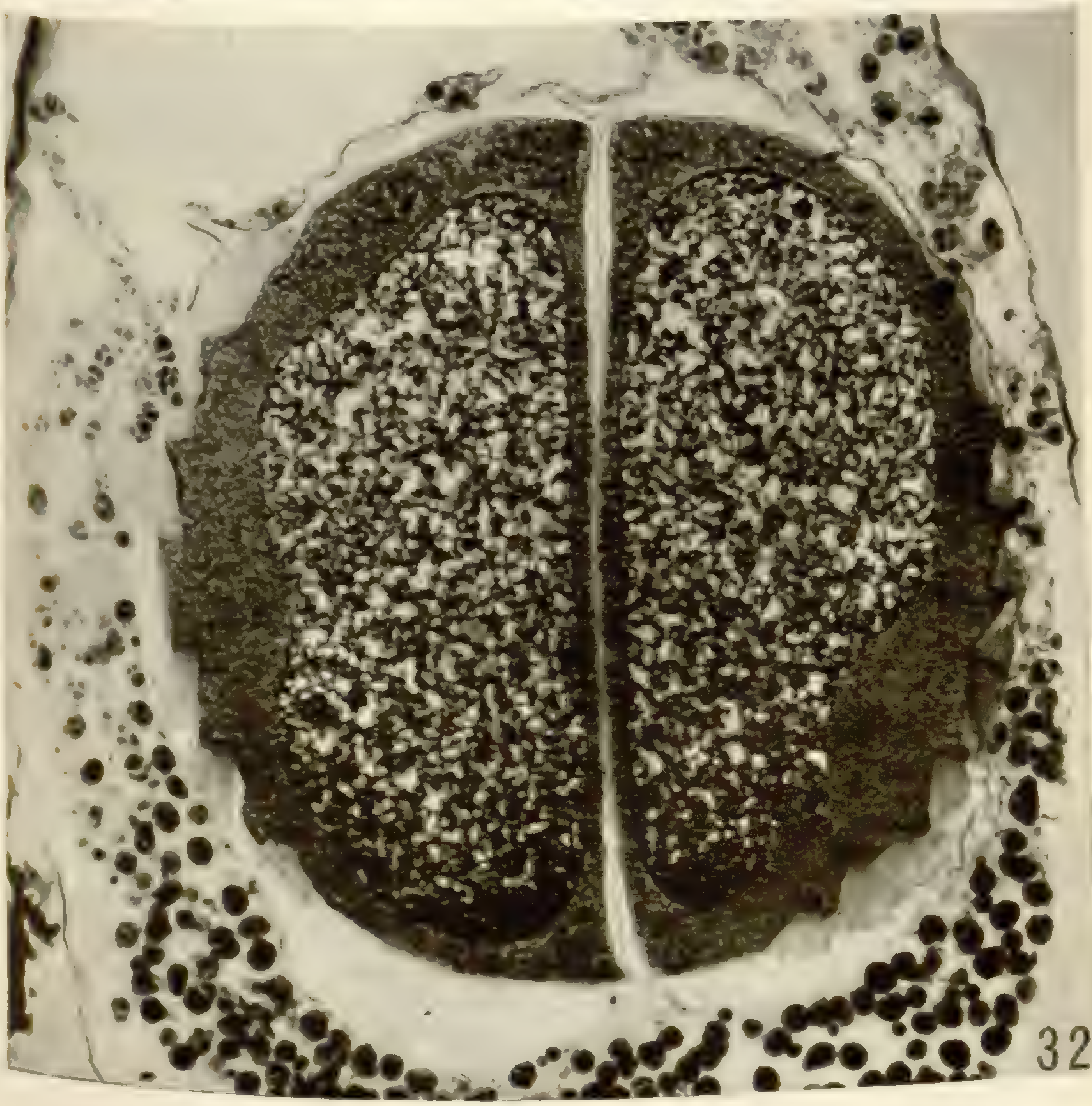

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CHAMBERLAIN on DIOON

BRIEFER ARTICLES

THE MOUNTING OF ALGAE

In a personal communication from the well-known phycologist Professor G. S. West, of the University of Birmingham, England, I received an outline of a method of fixing, mounting, and preserving algae which, as he tells me, has not been given the attention that it perhaps deserves. The fluid used serves at the same time as a killing, fixing, preserving, and mounting medium, and for delicate structures like desmids and other algal forms, it perhaps cannot be surpassed. It has the advantage, moreover, that it keeps the natural coloring of the green algae, something which the instructor in elementary laboratory work will appreciate better than anyone else. The fluid is a 2 per cent. solution of potassium acetate, just made blue with a small amount of copper acetate. The substance reduces plasmolysis of the cell contents to a minimum. The algae can be put into the solution and kept in it. If a permanent mount is wanted a small amount of the material is put on a rather thick slide and sealed with old gold size several times after each drying. The mounts are permanent, but it is usually necessary to take great care in sealing, and to this end to use a thick slide. A thin slide will bend considerably in handling, and the sealing may be separated in this way from the slide, so that the preparation will dry up as the result.

For some reason the fluid presents considerable difficulty with Vaucheria, and plasmolysis is hard to avoid. I have found that the best way to treat Vaucheria, especially the zoospores before or just after germination, when the plant is particularly delicate, is to kill it rapidly with 3 or 4 per cent. formalin. The formalin must be completely and quickly removed or the preparation will turn black afterward. Fixing for half an hour in the 3 per cent. formalin will not be injurious. Remove the formalin by repeated washing with water. If the Vaucheria thus treated is rapidly brought into glycerin to which a little thymol is added, the preparation will be as perfectly green as when alive, and will retain its green color indefinitely. The method may be extended to all small green forms like the smaller liverworts, fern prothallia, and moss protonemata.

To get the material into glycerin, add first a considerable quantity of 5 or 10 per cent. glycerin in water, and put the dish near but not on a radiator. In a few days the evaporation will leave the fluid thick. Once the preparation is in thick glycerin the color will not change, if the formalin has been completely removed.

The potassium-copper-acetate solution will not keep the natural color of diatoms. It has the property of removing the diatomin or yellow coloring matter from the diatoms and leaving the plants perfectly green. The solution can thus be used in demonstrating the presence of chlorophyll in these plants. The diatomin is removed or absorbed in a few minutes after application.

As I have found some difficulty in keeping the microscopic mounts made in the potassium-copper-acetate solution because of drying, I have evolved a modification of the glycerin method in combination with it. The mounts made by this method are perfectly durable, and when carefully prepared are superior to ordinary glycerin mounts, as all green algae treated with it keep their natural colors indefinitely. Glycerin jelly can also be used at the end to make the mount even more durable than the ordinary glycerin mount would be. The procedure is as follows.

The algae to be used are fixed in the potassium-copper-acetate 2 per cent. solution. After they have been killed and fixed in this fluid (the time varying according to the specimen treated), add to the above solution an equal part of 10 per cent. glycerin solution and allow to concentrate by evaporation in a warm dry place protected from dust. The algae must be thoroughly separated from dirt and soil or the concentrated solution will precipitate a reddish-brown cloud of reduced copper. In nearly all cases the preparation when thickened will be covered with a film of acetates, which can be removed from the top of the fluid without injury to the material. The concentrated solution should be perfectly clear, of a light green color, and the chromatophores of the algae as perfect a green as in life. I have often been asked by students, and in fact by those well acquainted with algae, whether the plants thus given them for examination were not really alive. The advantage of having plant material, especially for elementary students, in a condition as near as possible to the live state, obviates explanations about stains. I have found it very undesirable to give beginners any material other than alive or such as looks like the live stage of the plant studied.—J. A. Nieuwland, *University of Notre Dame, Ind.*

PAUL HENNINGS

(WITH PORTRAIT)

Professor **Paul Hennings**, the well-known mycologist, died after a short illness on October 14, 1908.

In the botanical circles of Berlin he was a welcome and esteemed personage, having won the sympathy of his colleagues by his extensive learning as well as by his kindly and unassuming nature. He was a distinguished collector and preparator, an authority on the world's fungi, a faithful and conscientious official of the Museum, and last, but not least, a gifted and humorous dialect poet.

As his personality and his whole nature were made up of a multitude of contradictions, understood only by those who knew him intimately, so the course of his development also shows many contradictions which alone give the key to a comprehension of this unusual man, who was, in the best sense of the word, an original.

Paul Hennings was born on November 27, 1841, in Heide, Dithmarsischen, Holstein. He grew up in provincial surroundings, attending the gymnasium at Meldorf until circumstances compelled him in 1860 to give up the scientific career to which he aspired, and to leave school when only a third-form boy.

He became an assistant in the Kiel botanical gardens and soon an acknowledged authority on the endemic flora. Professor **Nolte**, at that time director of the gardens, gave much attention to the aspiring young man, and ever afterward looked out for his interests in the most fatherly manner.

Urged by his older countryman, the Low-German poet **Klaus Groth**, with whom he was always on the most friendly terms, he was matriculated in Kiel in the winter semester of 1863–1864. The breaking-out of the war in 1864 obliged him to give up his work in Kiel, and he secured an official position in the post-office at Augustenburg. After many changes of residence he was transferred to Hohenwestedt where he remained until 1874. His official work was repugnant to him, and during this whole time he remained faithful to his love of science, teaching in the agricultural school of Hohenwestedt and soon taking a prominent position as a collector. In addition to all this work he began to issue not only his herbaria for agricultural purposes, but also the first hundred of his comprehensive seed collections.

In 1874, he was called by EICHLER, who at that time was director of the botanical garden at Kiel, to be his assistant. Here he put in order the LUCAS herbarium and devoted himself with great zeal to the cryptogamous herbarium. EICHLER was called to Berlin in 1879, and in 1880 he invited Professor HENNINGS to join him, and confided to him the arrangement of the newly established exhibition museum of the cryptogamous herbarium. While doing this he was also busy in the gardens. His power of application made it possible for him to complete speedily the work assigned to him.

From about 1885 he devoted himself almost exclusively to fungi. It is true that during this period he issued two fascicles of the algae of the Mark Brandenburg, but his interest centered in the mushrooms of this region, and later, when the museum received abundant collections from tropical regions, he devoted himself to the fungi of the whole world. His fine feeling for form enabled him in a short time to become an authority in all systematic questions regarding fungi. When in 1890 he was appointed assistant *Custos*, and in 1891 *Custos* of the Botanical Gardens, he had already brought together in Berlin one of the best collections of fungi in the world.

In 1902, as a well-deserved recognition of his work, he was appointed royal professor. Until his death he continued indefatigably at his work, the division of the fungi assigned him in the great museum.

Twelve months ago the death of his son paralyzed his energies and stole the pen from the busy hand.

HENNINGS in his special domain was self-taught, and his entire activity must be judged from this point of view. He possessed a fine sense of form, which made it possible for him at once to put every newly discovered species in the right place in the system. By this his work was greatly facilitated, and this explains his easy command, not only of the fungi of the Mark, but also of tropical regions. He published in twenty years 250 papers which dealt with the fungi of innumerable tropical regions. He made a specialty of the mushrooms of the German colonies and of Brazil. He dominated the difficult domain of the Hymenomycetes in a masterly manner, so that he discovered many unexpected treasures even at the gates of Berlin.

Few except those who stood near to this reserved—sometimes almost repellent—man, suspected that he had a really childlike soul, one particularly responsive to lyric poetry and to the dialect of his home. He wrote many humorous poems, revealing a rich poetical power, a deep comprehension of life, and a faithful devotion to his home.

He showed rare courteousness to his friends and even with strangers he was not parsimonious of his great knowledge. Helpful, modest, retiring, a man of the old stamp, of the right sort, has passed away with this scholar. Honor to his memory!—Translated from the German of LINDAU, by J. PERKINS, *Berlin.*

PURE CULTURES OF FUNGI

The *Association internationale des botanistes*, founded some years ago, has an office where pure cultures of fungi can be obtained either in exchange for others, or on payment. Although this fact is probably not unknown to the readers of this journal, we wish to remind them of it and state its exact purpose, trusting that more use will be made of the office than has been the case hitherto.

This office proposes to become a living register of the described fungi. Large numbers of species are mentioned in the handbooks, which are said to be insufficiently described and cannot possibly be identified. The number of identical species described under different names is immense. This evil may be avoided in future if every mycologist, when describing a new fungus, will send a culture to the office of the *Association*. The author not only is thereby relieved of its cultivation, but everyone who is studying kindred species may procure material for comparison.

Rather frequent applications are made to the office, but the collection does not grow in proportion to the description of new species. It has often happened that upon requesting a person to send us a culture of a certain recently described fungus, the author is obliged to reply that the cultures have been lost. Who can be sure ever to find again his fungus? The little trouble of sending it to the office, however, would have saved the original material to posterity.

But the office does not desire the new species only. Those also will be acceptable of which you have pure cultures and which are not mentioned in our list, published regularly in the *Botanisches Centralblatt;* because many species are asked for which we do not possess. You are requested to tell us whether the species left to our care need frequent renewing. The greater part of our cultures are transferred once every three months, but many of them need particular care.

Further information, and details of terms for the proposed service will be gladly supplied on application.—DR. JOHANNA WESTERDIJK, *I Roemer Visscherstraat, Amsterdam, Holland.*

CURRENT LITERATURE

BOOK REVIEWS

Physiological education

In putting out the second edition of his laboratory course in plant physiology,[1] Professor GANONG directs attention to its threefold purpose in these words:

> First, it aims to lead students through a good laboratory course in plant physiology. Second, it seeks to provide a handbook of information upon all phases of plant physiology having any educational interest. Third, I venture to hope that it may find service as a guide to self-education by ambitious teachers or students. . . . The book is not a compendium of physiological knowledge, nor yet, except incidentally, a handbook of investigations; but it is a guide to the acquisition of a physiological education. It is designed as a contribution to educational economy, and as such I wish it to be judged.

No one who examines the work can fail to see that it fulfils the threefold design of its author, so far as is compatible with success in making it, what it distinctly is, a contribution to educational economy, and by no means the first that Professor GANONG has produced. The strong pedagogical spirit which runs through the book is suffused by the even stronger scientific spirit, and the combination will make it of the highest service to teachers, as well as to those who, without other guidance, seek to gain a first-hand knowledge of plant physiology.

It must be pointed out that the book plans vastly more work than can be allotted to any elementary course in plant physiology in colleges. In the collateral lines of reading and inquiry that it suggests, there is opportunity for some years of labor, and for acquiring a wide knowledge of certain topics. Doubtless the author had it in mind that it is far better to err in this direction than to leave the student with the false notion that the book presents fully the whole subject. But a less informed and considerate teacher might heedlessly use such assignments to overburden seriously the conscientious student.

If, however, a self-taught student had this book alone as his guide, his knowledge of plant physiology might not be well balanced, because the pedagogical value of different parts of the subject, and hence the attention paid to them by the author, are not always proportionate to their importance. Thus, little more than 20 pages are devoted to the phenomena of irritability, and about an equal number to growth, while in both cases a considerable part of this is occupied by the description of apparatus. On the other hand, a little more than 20 pages is given to transpiration alone, and nearly twice as much to photosynthesis. While this allotment may be defended on pedagogical grounds, it is not clear that it is justifiable from the standpoint of the student or of the subject. Obviously, the author expects that by lectures or other reading and experimentation such inequalities are to be corrected.

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[1] GANONG, W. F., A laboratory course in plant physiology. 8vo. pp. vi+265. *figs. 68.* New York: Henry Holt & Co. 1908. $2.00.

One very helpful feature for the teacher is that various apparatus and methods of conducting experiments are either described in full or are referred to, so that they may be available. In most cases, however, it will be found that the method adopted in the book is clearly the most suitable for the elementary student, taking all things into consideration.

Much of the "normal apparatus," devised by Professor GANONG and now put upon the market, is highly convenient and useful. In some cases, however, it is doubtful whether the game is worth the candle, e. g., in the quantitative determination of transpiration; and often laboratory funds are more limited than the time of the student.

As to the particular course outlined in this guide, one must inquire whether, from the point of view of convenience, training, and knowledge acquired, the selection of experiments is the best that could be made, and whether appropriate attention is paid to the various topics. On these matters each teacher will have to form his own conclusion, because his own attitude toward the whole subject, and the special conditions under which his work is carried on, must be determining factors. Consequently, it is possible that no two would precisely agree. But we fancy there will be small disagreement with the statement that no one will fail to find this book of the greatest service in conducting elementary courses, even if he hesitates to adopt it formally as a laboratory manual; and for that purpose it is, in many respects, far and away the best that has appeared in any language.—C. R. B.

MINOR NOTICES

Javanese fresh-water algae.—Various works have contributed to make known the algal flora of Java, of which the nearly simultaneous ones by DE WILDEMAN and by GUTWINSKI are best known and most comprehensive. BERNARD, though not a professed phycologist and modestly decrying the value of his work, adds very materially to the knowledge of the Protococcaceae and Desmidiaceae, in a rather voluminous paper published by the Department of Agriculture of the Dutch Indies.[2] Beginning the work of collecting almost accidentally, the beauty and interest of the unicellular forms and the necessity of examining them in the living condition determined his study of them. In an introduction (45 pp.) the author, after giving briefly the history, bibliography, methods of study and collection, and the peculiarities of the localities explored, discusses the variations, adaptations, and cosmopolitanism of certain forms, states his attitude on nomenclature, and sets forth in tabular statistical form the various contributions to his subject. From this it appears that there are now known 230 species and varieties of these two orders, of which BERNARD has collected and described 202. Of these 4 are new to Java, 79 others are new to the East Indian region, and 81 are described as new species or varieties. By 580 carefully drawn figures, rather crowded on the plates, the author represents all species of his collection, so that later workers can see what plants he has actually been working with. The evident care and thoroughness of the work indicate that this is no mean contribution to the knowledge of the Javenese flora.—C. R. B.

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[2] BERNARD, CH., Protococcacées et Desmidiacées d'eau douce, recoltées à Java et decrites par C. B. Imp. 8vo. pp. 250. *pls. 16.* Batavia: Landsdrukkerij. 1908.

Folk names of Brazilian plants.—For some years there has been running through the *Pharmaceutical Review* a series of articles by Dr. THEODOR PECKOLT, giving the vernacular names of Brazilian plants and plant products, including both the Portuguese names and those adopted from the Tupi language. This material is now brought together in book form,[3] as monograph no. 15 of the Pharmaceutical Science Series, under the editorship of Dr. EDWARD KREMERS. The vernacular names appear in alphabetic order, with the German equivalent where it exists, the scientific equivalent, including the specific name and family name, when known, and brief comments in German on the use made of the products. It is rather unfortunate that there is not an index to the scientific names, for this would undoubtedly greatly increase the usefulness of what has been a difficult and time-consuming task. The volume will be of special assistance to taxonomists, to dealers in crude drugs, and to manufacturers who call for Brazilian products.—C. R. B.

German South-polar Expedition.—The second part of the eighth volume (Botany) of the sumptuous report upon this expedition has just been issued,[4] with an account by REINBOLD of all the seaweeds except the Lithothamniaceae, which are elaborated by FOSLIE. The collections were not extensive and no new species were found by REINBOLD. FOSLIE, however, recognized and described several new unsegmented corallines from the material obtained by this expedition, and here presents again the descriptions with photographic illustrations.—C. R. B.

NOTES FOR STUDENTS

A primitive type of seed.—OLIVER has made a most interesting contribution[5] to our knowledge of the structure of paleozoic seeds. In 1875 WILLIAMSON described *Physostoma elegans* from the Lower Coal-measures, but a little later placed it in his new genus Lagenostoma as *L. physoides*. OLIVER now proposes to revive the genus Physostoma as distinct from Lagenostoma, replacing the name *L. physoides* by the original *P. elegans*, and associating with it ARBER'S *L. Kidstonii* as *P. Kidstonii*.

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[3] PECKOLT, THEODOR, Volksbenennungen der brasilianischen Pflanzen und Produkte derselben in brasilianischer (portugiesischer) und von der Tupisprache adoptirten Namen. 8vo. pp. 252. Milwaukee: Pharmaceutical Review Publishing Co. 1907.

[4] Deutsche Südpolar-Expedition, 1901–1903, im Auftrage des Reichsamtes des Innern herausgegeben von ERICH VON DRYGALSKI, Leiter der Expedition. VIII. Band, Botanik, Heft II. (1) REINBOLD, TH., Die Meeresalgen, pp. 179–202. (2) FOSLIE, M., Die Lithothamnien. pp. 203–220. *pl. 20. figs. 1–6.* Berlin: Georg Reimer. 1908. *M* 5.

[5] OLIVER, F. W., On *Physostoma elegans* Williamson, an archaic type of seed from the Palaeozoic rocks. Annals of Botany **23**:73–116. *pls. 5–7. figs. 10.* 1909.

Physostoma elegans is remarkable in several particulars. It is a small (5.5–6^{mm}), narrow, usually ten-ribbed seed, with the integument free only in the region of the nucellar beak, as in Lagenostoma; but in this free region the integument consists of ten distinct lobes ("tentacles" the author calls them). These lobes are the direct prolongation of the ribs below, and represent the units of the "canopy" of Lagenostoma. Both lobes and ribs are clothed with long, club-shaped hairs. The testa shows no stony layer, and therefore is homogeneous, consisting of five or six layers of close-fitting, thin-walled, elongated cells. The vascular system enters the narrowed base of the seed as a single strand, which at once breaks up into a ring of strands, each one of which traverses a rib and continues on through the corresponding free lobe. The vascular strands lie along the inner limit of the integument, in what would be the "inner fleshy layer" had the usual three-layered differentiation of the testa occurred. On the outside of each strand there is a lacuna; and in the base of the seed a continuous lacuna surrounds the single large strand and the group of separating strands. It is suggested that these lacunae represent the position of disorganized phloem.

The nucellus is remarkable in its peripheral "secretory zone," which extends from the chalaza to the tip of the nucellar beak. The "secretory sacs" are thin, oblong, tabular cells, separated by a tissue of smaller cells. They are most abundant and crowded in the funnel-shaped region of the chalaza bounded by the diverging vascular strands and the base of the embryo sac. The author sees in the presence of these secretory sacs the retention in the ovule of a feature present in the vegetative organs, in which character Physostoma is unique in the Lagenostoma group. Between the secretory zone and the sac there is a tissue of six or more radially compressed layers, which the author calls the "tapetum." Of course this may represent the active nutritive zone developed in many gymnosperms in the nucellar tissue surrounding the sac; or it may be the ordinary nucellar tissue compressed by the enlarging sac. The megaspore membrane was only occasionally detected, and then as a very delicate one. The pollen chamber, as in Lagenostoma, is formed by the separation of the epidermis of the nucellar beak from the subjacent tissue, giving the appearance of nucellar tissue growing into the pollen chamber as a conical mass, the chamber thus becoming a bell-shaped crevice. Physostoma differs, however, from Lagenostoma, in the fact that the embryo sac invades this beak, so that the apex of the sac is invested by the base of the pollen chamber ("like the incurved bottom of a wine bottle"). OLIVER suggests that this apical prolongation of the sac of Physostoma may be the "primordial tent pole," as found in Cordaitales and Ginkgoales.

The pollen chambers contain an abundance of pollen grains, which show the cell-complex now known in several paleozoic seeds. The author thinks that at least the larger of these cells produced sperms, and asociated bodies, probably representing sperms, were also found.

The author concludes that an integument of free segments is more primitive than that of "coalesced" segments, and that probably intermediate stages of coalescence occur in the Lagenostoma group. In this group, therefore, the origin of the integument is multiple, but the nature of the units is the residual question. OLIVER is not inclined to accept Miss BENSON'S suggestion that the integument (as illustrated by that of *Lagenostoma Lomaxii*) has arisen by the sterilization of the peripheral sporangia of a synangium; but prefers to regard it as a new structure, arising contemporaneously with the seed habit, and related in some way to the "encasement" that so often accompanies reproductive activity.

The reasons for regarding Physostoma as a member of the Lagenostoma group are given in detail, and the conclusion is reached that it is the "most primitive seed yet come to light," the plant to which it belongs probably being one of the Lyginodendreae. The reasons for the conclusion quoted above are not quite clear, and seem to contradict some rather convincing conclusions reached by the same author in his study of Stephanospermum and other paleozoic seeds.—J. M. C.

Sterility in hybrids.—TISCHLER[6] has a lengthy treatment of the subject of sterility in hybrids. A preliminary paper, summarizing his conclusions, has already been reviewed in this journal.[7] The present paper is in two parts, the first presenting the cytological data and the second dealing with the theoretical conclusions. The use of charcoal in drawings can scarcely be recommended for clearness, many of the figures being mere smudges, and they furnish no sufficient evidence of such cytological matters as the pairing of threads in synapsis. Pollen formation, and in some cases megaspore formation, is described in hybrids of Mirabilis, Potentilla, and Syringa. A variety of irregularities, such as are common during the reduction divisions in hybrids, are described, including formation of extra nuclei by chromosomes left in the cytoplasm and failure of one or both reduction mitoses. In other cases the reduction processes were normal, but there was a lack of cytoplasm and the pollen grains failed to grow. *Potentilla rubens*, cultivated in dry and hot conditions, matured good pollen, but after fertilization the young embryos died. In all cases a paucity of cytoplasm was observed, beginning during or after reduction.

TISCHLER concludes that the cause of sterility is not any lack of harmony between the chromatic elements. However, it seems necessary to assume some "incompatibility" of the chromatins or plasms, which makes itself evident during the formation of reproductive cells, for otherwise there is no explanation why a plant continues to show vegetative growth and yet fails to mature its germ cells. Instead of a chromosome incompatibility, perhaps we may have in the cytoplasm some process which is symbolized by the pairing of chromosomes in synapsis, and which, owing to differences in the composition of the parental idioplasms, leads to derangement and finally cessation of the metabolism that had previously been carried on successfully. Some such hypothesis is necessary to explain why failure of growth usually begins with germ cell formation, and the necessity is not lessened by the fact that sterility is a purely relative phenomenon produced also by other conditions than hybridization.

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[6] TISCHLER, G., Zellstudien an sterilen Bastardpflanzen. Arch. Zellforschung 1:33–151. *figs. 120.* 1908.

[7] BOT. GAZETTE 45:68. 1908.

TISCHLER agrees with JOST that the increased luxuriance of some hybrids is probably due to a "poisoning" effect of one species on the other. Some of the cases of self-sterility bear a similar interpretation.

Three classes of facts are cited to show that there is not a segregation of characters during reduction in Mendelian hybrids: (1) Cases of vegetative splitting, as in *Syringa correlata* and *Cytisus Adami*. (2) Certain cases of latency or cryptomery (TSCHERMAK); e. g., the crossing of two white forms having certain other characters gives a violet hybrid. But such cases have been otherwise explained by the Mendelians. (3) Characters mendelize which cannot be represented by distinct portions of the idioplasm. Here are cited annual and biennial races of *Hyoscyamus niger*, immunity and non-immunity to rust in certain grains, and sterility and non-sterility in Lathyrus. On the other hand, it might be said that if the chromosomes are unlike, then each must represent some general property of the whole organism, if it represents anything. TISCHLER concludes that in the reduction divisions there is not a true segregation but latescence (*Latentwerden*) of characters. It is questionable whether this is an improvement over the idea of chromosomes or representative particles in the dominant and recessive condition in the germ cells, a hypothesis which will undoubtedly have to be given up. *Drosera rotundifolia* × *longifolia* produces pollen grains in tetrads, and in some cases two grains of a tetrad have characters belonging to each parent. This indicates a splitting of characters during reduction. But BATESON crossed races of Lathyrus having long and round pollen, in which all the F_1 had long pollen and the F_2 gave long:short in the ratio 3:1. From this it appears that it is possible to have Mendelian behavior without segregation of characters during reduction.

The frequent sterility in mutants, accompanied by similar irregularities to those in hybrids during reduction, as the reviewer has shown,[8] TISCHLER also ascribes to some disturbance of the idioplasm.—R. R. GATES.

Temperature and growth.—Beginners in research will do well to study this paper by BALLS.[9] It is of a type really too rare. It shows how a keen scientific discernment is alert to appreciate the significance of a casual observation in its bearing upon a fundamental problem. It shows how difficulties may be overcome by ingenuity in devising efficient apparatus and illustrates the potency of logical inquiry. One unfavorable criticism is that the scientific name of the organism is not given. During a study of a pest of the cotton crop in Egypt, the author noted that cultures of this "sore-shin" fungus showed a notable difference between the thermal death-point and the temperature inhibiting growth. This observation suggested an analysis of the temperature factor in its effects upon growth. It is stated that the hyphae of this fungus are morphologically and physiologically equivalent, in that spore-formation, sexual or asexual, does not occur. Of course this statement is not to be taken literally, as it would be very difficult to say that all the hyphae of a given fungus are physiologically equivalent. As a matter of fact, the author himself states that in liquid cultures at 20° C. resting cells are formed in abundance. If the cultures are grown at 34° C. growth ceases (culture becomes stale) much earlier than at lower temperatures. This feature of "staleness" or of discontinued growth was found to be caused by the accumulation of substances which retard and if sufficiently concentrated stop growth. The substance or substances which originate in the organism as a result of the effect of temperature, and whose influence is to inhibit growth, have been isolated from the organism as products of katabolism, though they have not been chemically identified. To such katabolites the provisional name of "X" is given. From a large number of tests whose results are tabulated, illustrated by appropriate curves and verbally discussed, it appears to be demonstrated (*a*) that with increasing temperature there is a regular acceleration in the rate of growth up to 30° C. and this acceleration approximately fulfils the expectation based upon VAN'T HOFF's law; (*b*) above 30° C. the growth-rate acceleration decreases as the factor of time becomes limiting; (*c*) later growth stops at a fairly definite temperature, which the author proposes to call the "stopping point;" (*d*) the optimum is therefore not a definite temperature but a status of the organism in which the effects of the factors of time and of temperature physiologically balance. As would be expected the style and composition of the paper are consistent with the logical development of the investigation.—RAYMOND H. POND.

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[8] GATES, R. R., Pollen development in hybrids of *Oenothera lata* × *O. Lamarckiana*, and its relation to mutation. BOT. GAZETTE **43**:81–115. *pls. 2–4.* 1907.

[9] BALLS, LAWRENCE W., Temperature and growth. Annals of Botany **22**:557–591. 1908.

Seedlings of conifers.—With the hope of finding facts of phylogenetic importance, HILL and FRAINE began, some time ago, a comparative study of the transition region in seedlings. Their preliminary announcement of results was noted in this journal;[10] the first paper of the series has appeared recently.[11]

The species examined in this part of the work are included in thirteen genera of the Coniferales. Two subfamilies of the Taxaceae are represented, the Podocarpineae and the Taxineae; and of the Pinaceae two subfamilies, the Taxodineae and the Cupressineae. In all the conifer seedlings examined the authors find the transition to be according to VAN TIEGHEM's type 3 or a modification of it. In all but Podocarpus, which has two, there is only one vascular bundle in each cotyledon. The cotyledonary bundles contain either centripetal xylem or its lineal descendant, transfusion tissue, the pronounced mesarch bundle occurring in greater proportion in the Taxineae (Taxus and Cephalotaxus). With respect to the number of cotyledons, only members of the Pinaceae (Cryptomeria and *Sequoia gigantea* in the Taxodineae, and Libocedrus and some species of Cupressus among the Cupressineae) have more than two. The presence of resin ducts, likewise, was observed only in the Pinaceae, Juniperus having them in the leaves, and the Taxodineae having them in the cotyledons in all the forms examined, except Widdringtonia. Two instances of fusion of cotyledons are reported: in *Widdringtonia Whytei*, the two cotyledons unite laterally to form one, recalling the leaf of Sciadopitys; in *Cupressus torulosa*, the cotyledons fuse near the base to form a tube. In every case the number of root poles corresponds with the number of "whole" cotyledons.

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[10] BOT. GAZETTE **43**:77. 1907.

[11] HILL, T. G., AND FRAINE, E. DE, The seedling structure of gymnosperms. I. Annals of Botany **22**:689–712. 1908.

The authors believe that dicotyledony is the more primitive condition, and that the polycotyledonous form has been derived from it by splitting; but the statement of their reasons for this conclusion is deferred to a future paper.

It is a hopeful sign that the authors did not intrust this valuable collection of seedlings to the mercy of a razor; to read that the sections were made in an orderly fashion with the help of a microtome gives double assurance that the observations are accurate.—HELEN A. DORETY.

Root excretions.—STOKLASA and ERNST[12] report a conclusive piece of work on root excretions. The excellent technique these workers have developed in handling similar problems makes their contribution in this much disputed field unusually valuable. They find that no acid (organic or inorganic) except H_2CO_3 is excreted by roots, if they are fully supplied with oxygen, so that aerobic respiration is unrestrained. In limited oxygen supply, certain organic acids are formed and excreted; but in no case is any inorganic acid or salt excreted; not even monopotassium phosphate, contrary to the claim of CZAPEK. The organic acids appearing under limited oxygen supply vary with the plant used. Buckwheat and barley give formic and acetic acids; oats and maize, formic; and the beet, oxalic. STOKLASA and ERNST believe these acids arise from the incompletely oxidized products of respiration. In a full oxygen supply they maintain that these acids are oxidized to carbon dioxid and water.

The authors are to make an exhaustive investigation of the question whether any hydrogen is produced in the aerobic respiration of roots, and what organic acids are excreted by the roots of many other species of plants under limited oxygen supply.

The authors also determined the amount of CO_2 excreted by the root systems of barley, oats, rye, and wheat. The barley root-system gives off the greatest amount of CO_2 and produces the greatest dry weight. The quotient arising from dividing by the dry weight of the root system the weight of CO_2 produced is least in barley and greatest in oats. This quotient is considered as the indication of the specific energy of respiration.

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[12] STOKLASA, J., AND ERNST, A., Beiträge zür Lösung der Frage der chemischen Natur des Wurzelsekretes. Jahrb. Wiss. Bot. **46**:55–102. 1908.

The authors point out that the injury to farm crops by insufficient aeration of the soil probably arises from the accumulation of the highly toxic organic acids due to the incompletely oxidized products of respiration.

It should be mentioned here that the authors have studied only the aliphatic excreta and make no mention of any of the aromatic series.—WM. CROCKER.

Graft hybrids.—The question of the occurrence of graft hybrids has long been undecided, and the possibility of their existence has even been denied. WINKLER undertook an extensive series of experiments on this subject, using as material two species which will not hybridize in the ordinary manner, namely *Solanum nigrum* and *Solanum lycopersicum*. In an earlier paper[13] he dealt with the production of what he calls chimeras, that is shoots, one side of which resembles either parent, the cells of the two parents growing in juxtaposition without modifying each other. He has finally succeeded[14] in producing a true graft hybrid between the same species by the same method.[15] In all, 268 grafts were made, which after decapitation produced over 3000 adventitious shoots. Five of the latter were chimeras and a single one a graft hybrid, which came from grafting *S. lycopersicum* on *S. nigrum*. After decapitation the cut surface of one graft produced 14 adventitious shoots, 8 of which were pure *S. nigrum*, 5 *S. lycopersicum*, and 1 the graft hybrid. The latter was detached and rooted, finally producing flowers. It is intermediate in character between the parents, though somewhat nearer *S. nigrum*. The purity of both parents was assured by using guarded "pure line" cultures. WINKLER names the hybrid *S. tubingense*, and proposes to use the sign + for graft hybrids instead of ×, the sign for a sexual cross. Two other adventitious shoots are also probably intermediate in character, one of them being nearer the *S. lycopersicum*.

STRASBURGER,[16] in a cytological study of the reputed graft hybrid *Cytisus Adami*, found the number of chromosomes to be the same as in each parent. Several interesting cytological questions, which WINKLER hopes to determine, are involved in the nuclear and chromosome behavior of his graft hybrid. Apparently there must be a union of cells, nuclei, or chromosomes, or perhaps of all three, in the production of this form.—R. R. GATES.

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[13] WINKLER, HANS, Ueber Pfropfbastarde und pflanzliche Chimären. Ber. Deutsch. Bot. Gesells. **25**:568–576. *figs. 3.* 1907.

[14] ———, *Solanum tubingense*, ein echter Pfropfbastard zwischen Tomate und Nachtschatten. Ber. Deutsch. Bot. Gesells. **26a**:595–608. *figs. 2.* 1908.

[15] Briefly described by the reviewer in BOT. GAZETTE **47**:84. 1909.

[16] STRASBURGER, E., Ueber die Individualität der Chromosomen und die Pfropfhybriden-Frage. Jahrb. Wiss. Bot. **44**:482–555. *pls. 5–7. fig. 1.* 1907.

Germs in the air.—SAITO has determined, by agar and gelatin plates, 10 in each experiment and exposed by the ancient method (cf. SEDGWICK and TUCKER, 12th Ann. Rep. Mass. State Bd. Health, Boston, 1889), the number of bacteria, as counted by colonies, and the kinds found in the University garden and the street air of Tokyo.[17] Several of these tests were made in each month of the year, with observations as to temperature, humidity, wind, etc. He found a high street average in July and August during a period of dust and dryness following a wet season. The garden average increased in November and December in proportion to a large number of windy days. Snow or rainfall always cleansed the air of germs. Of the 55 Bacteriaceae and 17 Coccaceae found, SAITO described 18 as new species, without making much attempt to relate these to forms already known. It is difficult to see, for instance, wherein his *B. rufulus* differs from *B. rubiginosus* described by CATAINO in COHN'S Beiträge **7**:538. 1896; and *Sarcina agilis* appears to differ from *M. agilis* as described by Migula in 1897 only in the easily lost character of pigment formation. Motile sarcinas, however, are rare and should be carefully studied.—MARY HEFFERAN.

Anatomy of Saxegothaea.—This monotypic conifer, restricted to the wet woods of the upper slopes of the Andes of Chili, has long been in demand for morphological investigation. When LINDLEY described it in 1851, he called attention to the transition characters it exhibits between Taxaceae and Pinaceae. Allied with the Podocarpineae in what are regarded as the more important characters, it shows even more resemblance to the Araucarineae than do the other podocarps, especially in its wingless pollen grains and distinct cone of spirally arranged sporophylls. STILES[18] has examined the anatomical structure of two specimens in cultivation in England, and concludes that the genus is relatively primitive. The structure of the wood of the stem and of the medullary rays is simple; and this, taken together with the simple arrangement of the sporophylls, has convinced the author that Saxegothaea is at least the oldest of the podocarps, and shows derivation from a common ancestral stock with the araucarians.—J. M. C.

Potato breeding.—EAST[19] considers the extensive record of the history of the potato, and future methods of its improvement. Many interesting biological facts of variation and hybridization in the potato are brought together, as well as practical suggestions for the improvement of varieties. The cultivation of other species of Solanum for tuber production has not been marked with success, but it is hoped that crosses of the common potato with *S. Commersonii* may produce varieties which are more resistant to disease. Methods of improvement include (1) crossing under controlled conditions, (2) selection of fluctuations, and (3) selection of wider variations and a study of ways of causing them, graft hybrids being a possible method.—R. R. GATES.

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[17] SAITO, K., Untersuchungen über die atmosphärischen Pilzkeime. Jour. Coll. Sci. Univ. Tokyo, **23**:no. 15. pp. 77. *figs. 19. charts 2.* 1908.

[18] STILES, W., The anatomy of *Saxegothaea conspicua* Lindl. New Phytol. **7**: 209-222. *figs. 28-34.* 1908.

[19] EAST, E. M., A study of the factors influencing the improvement of the potato. Ill. Agr. Expt. Sta. Bull. 127. *figs. 10.* 1908.

Salts of aluminum.—FLURI[20] finds that aluminum salts cause the disappearance of starch from Spirogyra and other water plants, even when they are well illuminated. It likewise renders the protoplasm permeable to ordinary plasmolytic agents. The disappearance of the starch is probably due to the joint action of three effects of these salts: loss of sugar through the permeable protoplasm, the increased diastatic action, and the slower photosynthetic activity. If glucose, glycerin, or isodulcitol is mixed with the aluminum salt, the salt does not then render the protoplasm permeable.—WM. CROCKER.

Transpiration and water storage.—SHREVE[21] finds that *Stelis ophioglossoides*, a water-storing epiphyte which grows at mid-height in the rainy forest of Jamaica, is less able to resist continued drought than *Guzmania tricolor*, an epiphyte which does not store water, but grows at the top of the rainy forest. Stelis reduces its transpiration almost to nothing when forced to draw upon the stored supply in the leaves. With an abundant external supply, it shows rather rapid and regular transpiration.—WILLIAM CROCKER.

Branch cankers of Rhododendron.—VON SCHRENK[22] describes some interesting swellings of the branches of *Rhododendron maximum* that are produced where dead twigs have fallen. The healing layer starts to develop at a distance from the base of the fallen twig, and in a few years a large swelling results. The chief interest in the phenomenon arises from the fact that a gall-like structure is produced without the intervention of a parasite.—H. C. COWLES.

Virescence in Oxalis.—HUS[23] has been studying plants of *Oxalis stricta* with bright green petals, but which are otherwise representative of the species. While the green petals approach sepals in structure in some respects, they retain other characteristics of the ordinary petals. The new form, which has been named *Oxalis stricta viridiflora*, is constant from seed, and is to be made the object of careful study.—H. C. COWLES.

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[20] FLURI, MAX, Der Einfluss von Aluminiumsalzen auf das Protoplasma. Flora **99**:81–126. 1908.

[21] SHREVE, FORREST, Transpiration and water storage in *Stelis ophioglossoides*. Plant World **11**:165–172. 1908.

[22] SCHRENK, H. VON, Branch cankers of Rhododendron. Mo. Bot. Gard. Rep. **18**:77–80. 1907.

[23] HUS, H., Virescence of *Oxalis stricta*. Mo. Bot. Gard. Rep. **18**:99–108. 1907.

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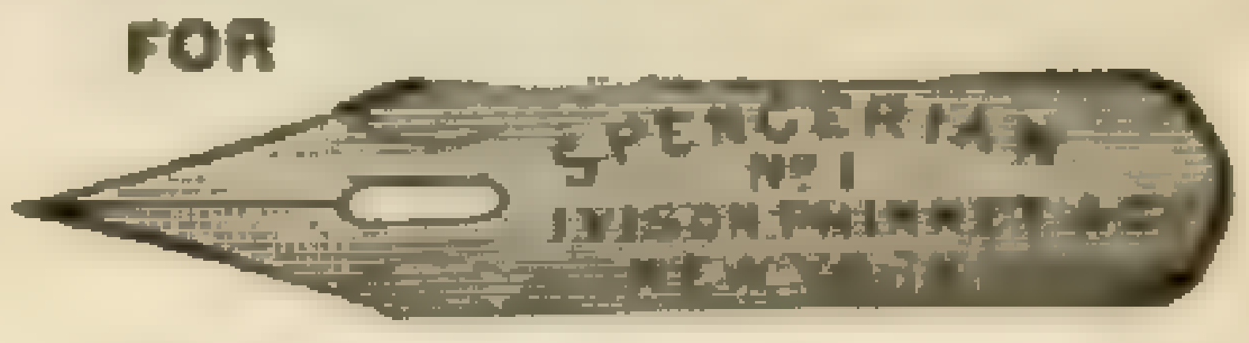

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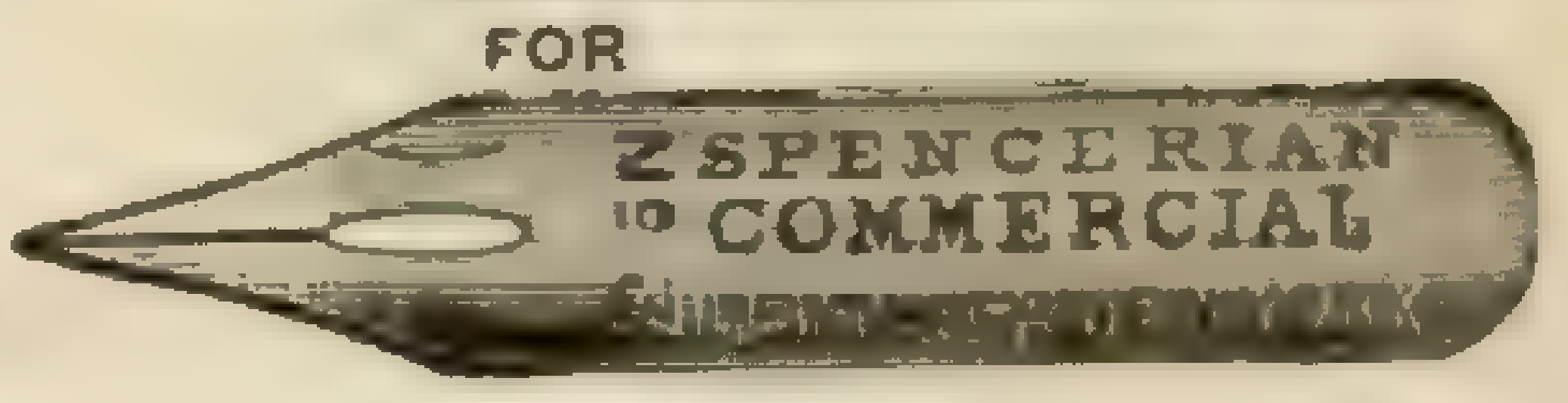

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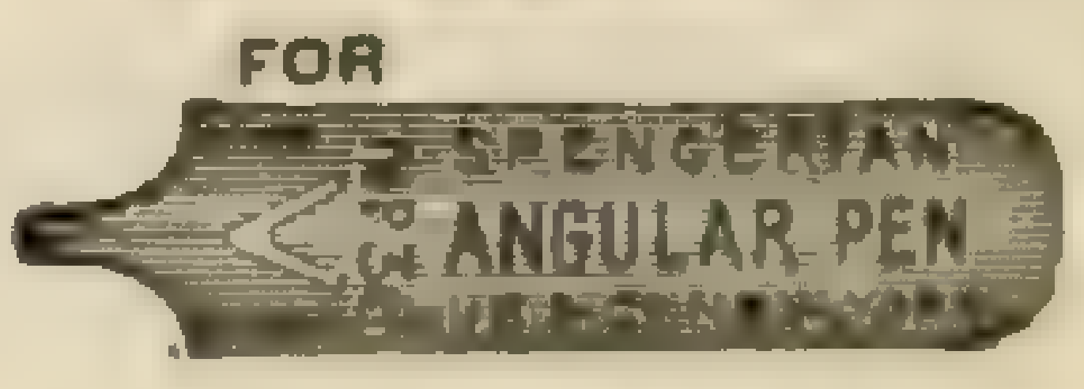

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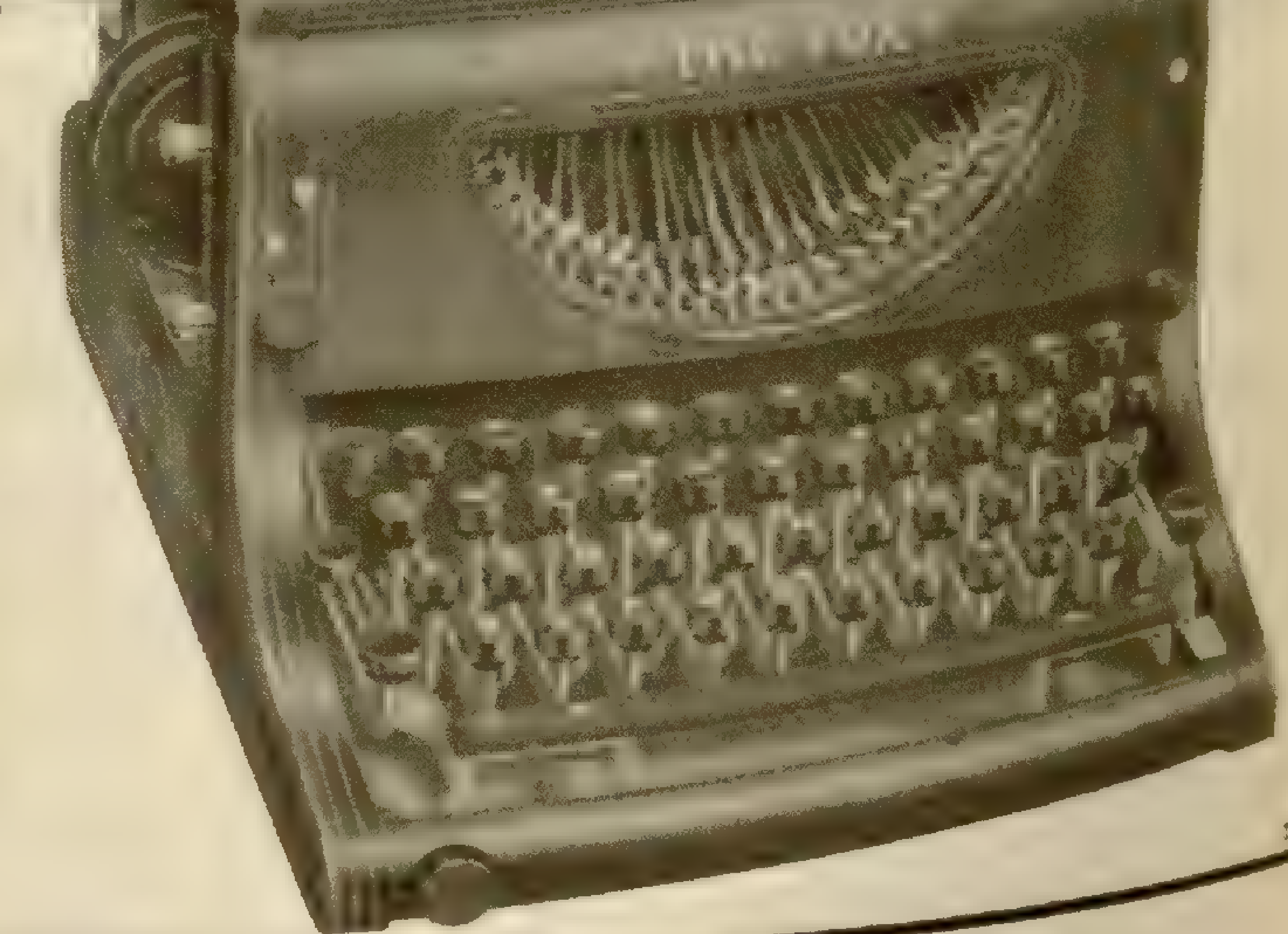

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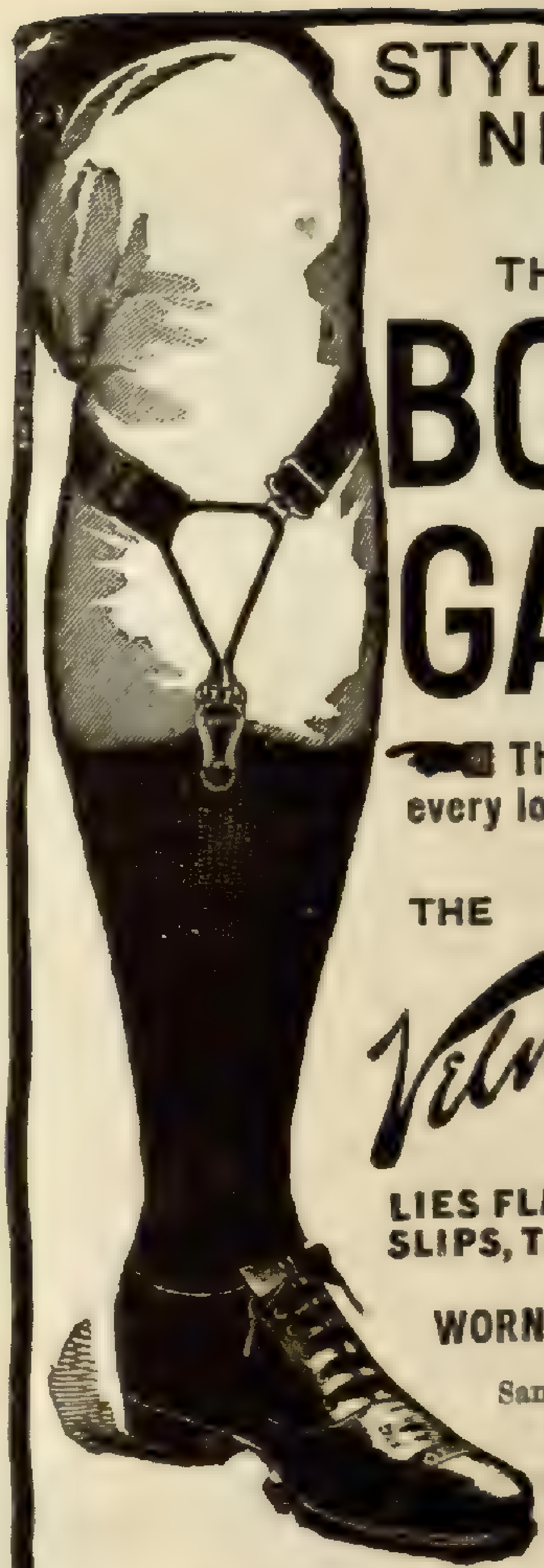

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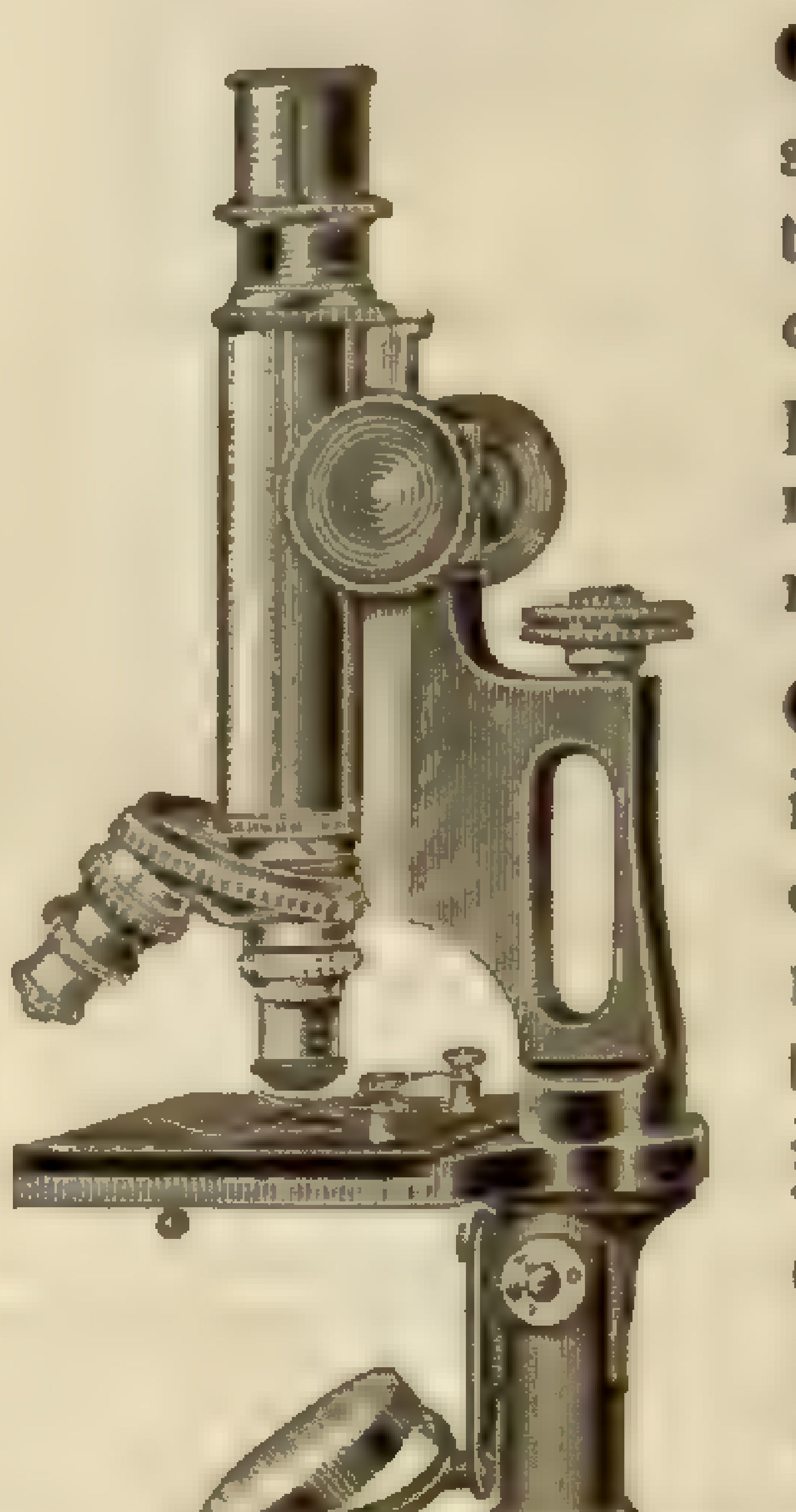

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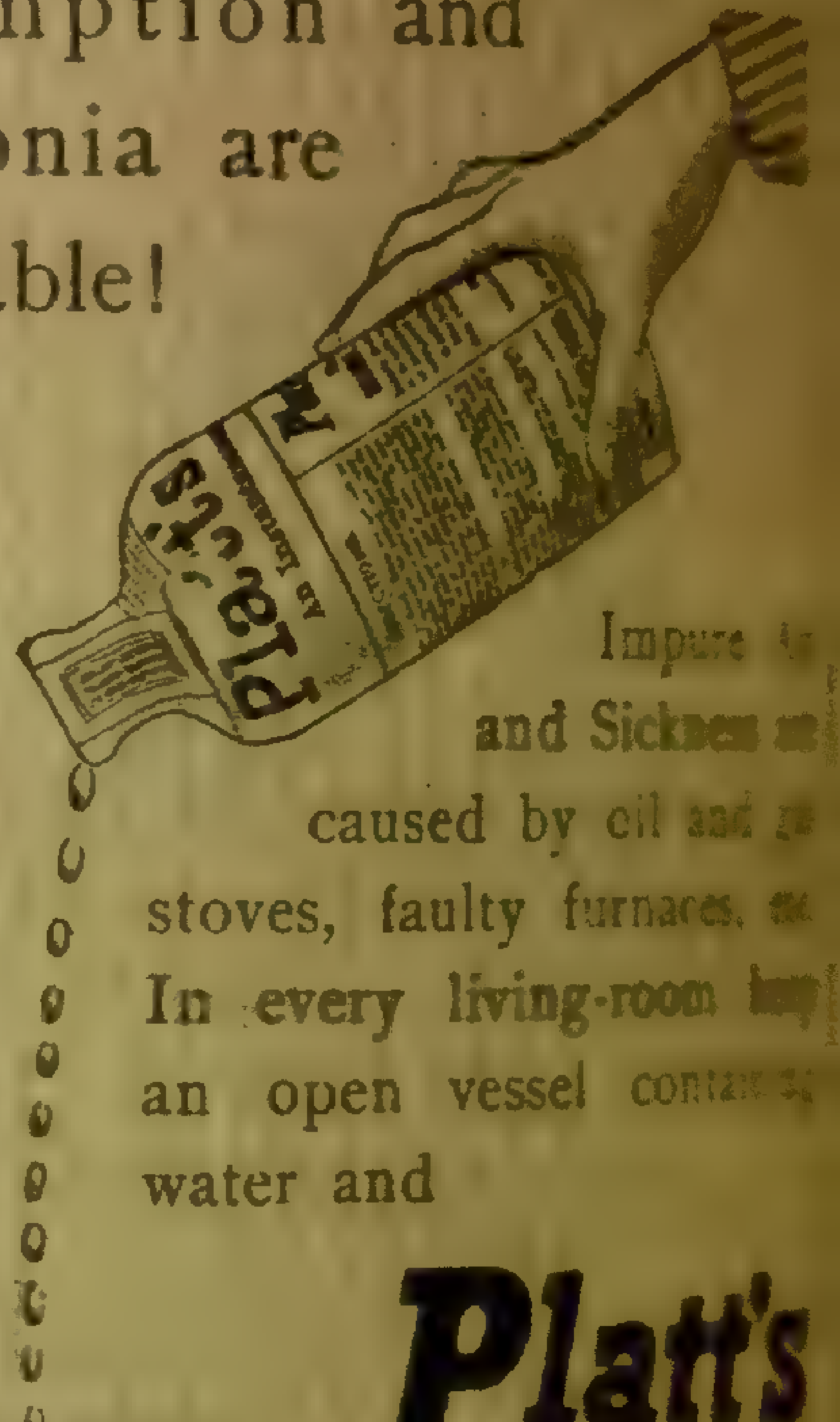

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THE
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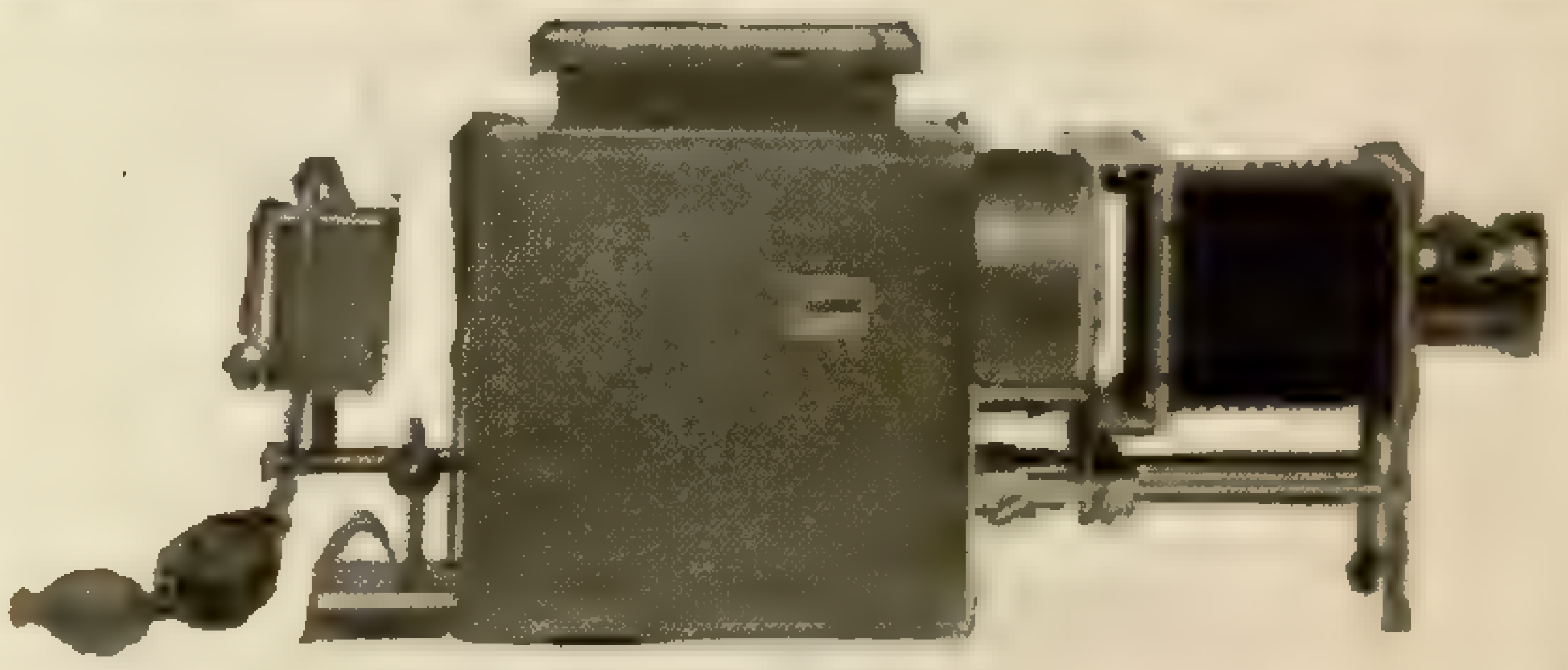

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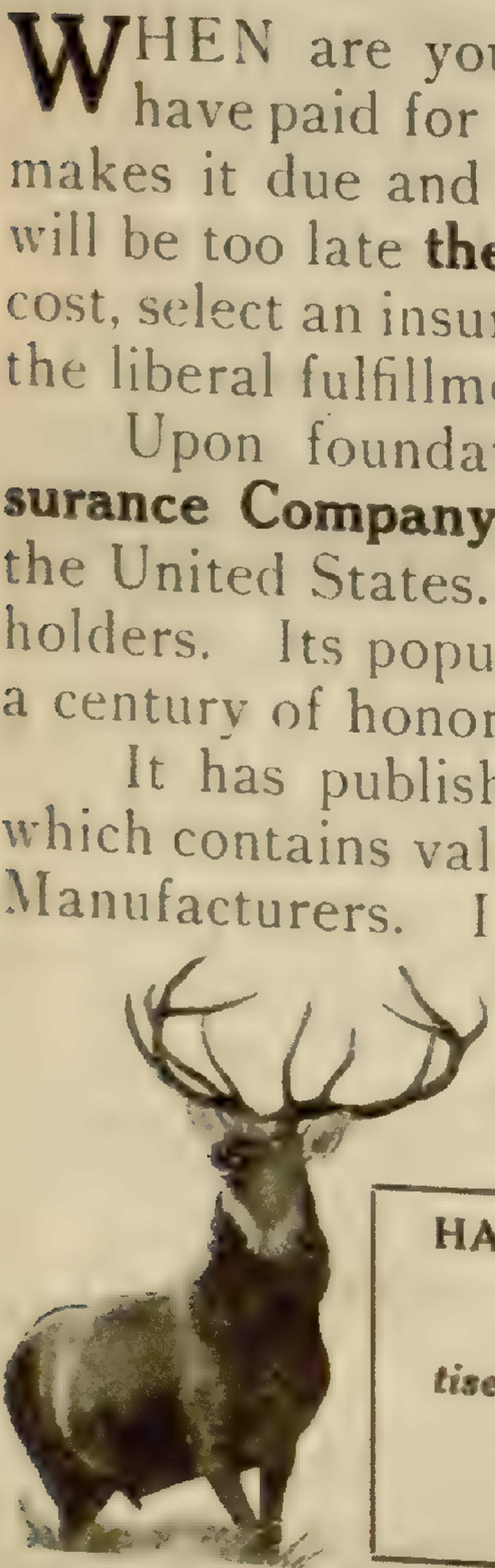

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UNDESCRIBED PLANTS FROM GUATEMALA AND OTHER CENTRAL AMERICAN REPUBLICS. XXXI[1]

JOHN DONNELL SMITH

(WITH ONE FIGURE)

Magnolia guatemalensis Donn. Sm.—Glabra. Folia breviter petiolata elliptica apice acuta basi obtusiuscula concoloria subtus glabrescentia crebre penninervia. Sepala oblonga tenuiter coriacea 5-nervia. Petala spatulato-obovata coriacea. Stamina numerosissima. Gynophorum fusiforme.

Arbor 6–8-metralis. Folia supra cum ramulis petiolis pedunculo glabra subtus pilis sparsis castaneis aspersa vel denique glabra 12–16^{cm} longa 5.5–8.5^{cm} lata plerumque abrupte breviterque cuspidata, costa subtus tuberculato-rugosa, nervis lateralibus utrinque 13–16, interjectis minoribus vix ullis, petiolis 1.5–2^{cm} longis apice canaliculatis ceterum teretibus. Pedunculus 3^{cm} longus, stipulis foliorum nascentium 8–15^{mm} longis passim castaneo-pubescentibus. Sepala 58–60^{mm} longa 21–22^{mm} lata ima basi 6–8^{mm} lata humectate pellucido-punctulata. Petala 65–70^{mm} longa 29^{mm} lata ima basi 2–3^{mm} lata opaca cum sepalis obtusa glabra nivea. Receptaculum staminale 6^{mm} longum 4^{mm}-diametrale, staminibus circiter 95. Gynophorum 25^{mm} longum medio 9^{mm}-diametrale, carpellis circiter 22–24 dorso sulcatis in stigma 4^{mm} longum recurvatum attenuatis. Fructus desideratur.—*M. portoricensi* Bello proxima differt praesertim glabritate.

In palude profunda prope Tactic, Depart. Alta Verapaz, Guatemala, alt. 1550^{m}, Mart. 1908, *H. von Tuerckheim* (n. II. 2165).

Marila verapazensis Donn. Sm.—Folia supra glabra subtus nervis puberula et diaphano-punctulata ceterum opaca oblonga acute curvilineo-cuspidata basi acutiuscula. Racemi folia subaequantes puberuli. Sepala ovata vel ovalia pedicellum aequantia petalis obovato-oblongis paulo breviora. Antherae in appendicem linearem productae. Stylus ovario vix brevior, stigmate minimo.

---

[1] Continued from BOT. GAZETTE 46:117. 1908.

Ramuli glabri. Folia coriacea 18–20^{cm} longa medio 6–6.5^{cm} lata, nervis subtus elevatis et pallidis, lateralibus parallelis utrinque 13–15 sub ipso margine arcuatis, venis transversis undulatis, venulis minute reticulatis, petiolis 12–15^{mm} longis. Racemi fere a basi floriferi prope basin ramum nonnunquam emittentes, pedicellis inordinatim dissitis puberulis, floribus pentameris. Sepala in alabastro puberula post anthesin deflexa 7–8^{mm} longa, 3 exteriora late obtuseque ovata interioribus suborbicularibus paulo angustiora. Petala 9^{mm} longa apice 3–4^{mm} basi 1^{mm} lata. Stamina 4–5^{mm} longa, antheris appendice eis paulo breviore computata 2^{mm} longis. Ovarium glabrum elongato-oblongum, stylo 5^{mm} longo, stigmate pyramidato 1^{mm} longo. Capsula ignota.—*M. macrophyllae* Benth. proxima.

In silvis montanis ad praedium *Cubilquitz* dictum, Depart. Alta Verapaz, Guatemala, alt. 350^{m}, Oct. 1904, *H. von Tuerckheim*, n. 8660 ex Pl. Guat. etc. quas ed. Donn. Sm.

Leandra (§CARASSANAE Cogn.) **Tuerckheimii** Donn. Sm.—Ramuli teretes uti petioli paniculae calyces strigillosi. Folia ovato-oblonga vel -lanceolata incurvo-acuminata basi acuta septuplinervia discoloria supra tuberculato-setosa subtus foveolata pubescentia. Flores ebracteolati. Calycis lobi interiores brevissimi, segmenta exteriora filiformia tubum aequantia.

Ramuli dichotomi. Strigillae densae arcte appressae purpurascentes. Folia leviter disparia rigida inter bullas diaphana supra intense viridia setis crassis curvatis armata subtus pallida nervis strigillosa venis pubescentia 7–11^{cm} longa infra medium 3–4.5^{cm} lata basi inaequalia, petiolis in eodem jugo inaequalibus 1.5–3^{cm} longis. Paniculae terminales singulae vel 2–3-nae trichotomae 6–7.5^{cm} longae, bracteolis lineari-lanceolatis 1.5–2^{mm} longis, pedicellis 1.5–2^{mm} longis, floribus 5-meris. Calyx longe strigillosus, tubo campanulato 3–4^{mm} longo infra limbum non constricto, lobis interioribus vix 0.5^{mm} longis semiorbicularibus. Petala oblongo-ovata 4–5^{mm} longa. Stamina 10, antheris 1.5^{mm} longis filamenta compressa aequantibus, connectivo infra loculos haud producto. Ovarium vertice convexo glabrum 5-loculare, stylo 4–5^{mm} longo. Bacca non adest.—Secundum methodum clari *Cogniaux* juxta *L. strigilliflorum* Cogn. locanda.

In summo monte silvestri prope Cobán, Depart. Alta Verapaz, Guatemala, alt. 1600^{m}, Jun. 1908, *H. von Tuerckheim* (n. II. 2369).

Hoffmannia Tuerckheimii Donn. Sm.—Pubes undique paleae- et monili-formis. Folia inter minora longiuscule petiolata ovata vel ovalia contracto-acuminata basi acuta vel rotundata supra nitida subtus prasertim ad nervis pubescentia. Flores fasciculati subsessiles pubescentes. Calycis tubus obovatus lobis subulatis bis longior corolla partita 6-plo superatus. Filamenta antheris triente breviora.

Ramuli dichotomi teretes lenticellati fusco-pubescentes, stipulis triangularibus. Folia coriacea 5–6.5$^{\mathrm{cm}}$ longa 2.5–4$^{\mathrm{cm}}$ lata subtus pallida et inter nervos subtilius pubescentia, nervis lateralibus utrinque 5–7, petiolis 15–22$^{\mathrm{mm}}$ longis. Pedunculus vix ullus nodiformis glandulosus, pedicellis 3–10-nis 1$^{\mathrm{mm}}$ longis, floribus tetrameris 14$^{\mathrm{mm}}$ longis. Calyx tetragonus 3$^{\mathrm{mm}}$ longus sinubus glandulosus. Corolla sparsius pubescens 12$^{\mathrm{mm}}$ longa, segmentis linearibus tubo 5-plo longioribus. Stamina fauci inserta 5$^{\mathrm{mm}}$ longa, antheris lineari-oblongis. Stylus corolla paulo brevior, stigmatibus 2 linearibus 2$^{\mathrm{mm}}$ longis. Bacca deest.

In silvis supremis montis prope Cobán, Depart. Alta Verapaz, Guatemala, alt. 1600$^{\mathrm{m}}$, Mart. 1908, *H. von Tuerckheim* (n. II. 2160).

Guettarda (§Ulolobus DC.) **cobanensis** Donn. Sm.—Folia ternatim verticillata longe petiolata oblongo-elliptica sursum subsensim deorsum contractius acuminata glabrescentia. Stipulae internodiis superioribus breviores. Flores 4–5-meri. Corolla inter longiores, tubo calycem 7-plo lobos proprios 3-plo stylum dimidio superante. Drupa glabra, putamine 3–4-loculari atque -quetro, lobis intermediis saepius adjectis.

Ramuli obtuse trigoni pubescentes, internodiis inferioribus 1$^{\mathrm{cm}}$ superioribus 2$^{\mathrm{cm}}$ longis, stipulis ovatis 5$^{\mathrm{mm}}$ longis extus medio intus undique cano-sericeis. Folia juniora supra fere glabra subtus nervis venisque appresse sericeis argentea, provectiora utrinque nitida 15–20$^{\mathrm{cm}}$ longa medio 7.5–9$^{\mathrm{cm}}$ lata, nervis lateralibus utrinque 12–13, venis transversis creberrimis pellucidis, petiolis pubescentibus 2–7$^{\mathrm{cm}}$ longis et foliis in eodem verticillo inaequalibus. Cymae pubescentes furcatae, pedunculo 1.5–2$^{\mathrm{cm}}$ longo, bracteis lanceolatis 1$^{\mathrm{mm}}$ longis, floribus sericeis. Calycis 3$^{\mathrm{mm}}$ longi limbus brevis dentatus persistens. Corollae tubus cylindricus 22$^{\mathrm{mm}}$ longus, lobi lacerato-crispati. Antherae 4$^{\mathrm{mm}}$ longae. Ovarium tetragonum, stylo 14$^{\mathrm{mm}}$ longo cano-pubescente, stigmate capitato. Drupa ovoidea 10$^{\mathrm{mm}}$ longa 7$^{\mathrm{mm}}$ lata calycis limbo coronata, putamine osseo profunde acuteque 3–7-lobato, loculis rectis.—*G. crispiflorae* Vahl proxima.

In silvis montanis prope oppidum Cobán, Depart. Alta Verapaz, Guatemala, alt. 1500$^{\mathrm{m}}$, Jan. 1908, *H. von Tuerckheim* (n. II. 2096).

Chomelia brachypoda Donn. Sm.—Inermis. Folia glabrescentia oblongo-lanceolata utrinque acuminata paucinervia transversim venulosa. Pedunculi petiolis parum longiores, cymis laxe paucifloris et floribus paene glabris. Calyx subsessilis oblongus minute denticulatus. Corollae tubus anguste cylindricus calyce 4-plo lobis propriis 5–6-plo longior.

Ramuli petioli stipulae pedunculi appresse pilosi, cymis calycibus corollae lobis sparsim pilosiusculis. Folia 7–10$^{\mathrm{cm}}$ longa medio 2.5–3$^{\mathrm{cm}}$ lata sursum tenuiter acuteque incurvo-angustata deorsum subsensim acuminata chartacea in sicco viridia supra glabra subtus pilis raris aspersa et axillis barbata, nervis lateralibus utrinsecus 4–5, venulis erga lucem inspectis manifestis creberrimis undulatis, petiolis 5–6$^{\mathrm{mm}}$ longis, stipulis filiforme linearibus 6–8$^{\mathrm{mm}}$ longis. Pedunculi 5–8$^{\mathrm{mm}}$ longi medio bibracteolati, cymis 4–8-floris, pedicellis brevissimis crassis. Calyx 2.5–3$^{\mathrm{mm}}$ longus, denticulis triangularibus vix 0.5$^{\mathrm{mm}}$ longis. Corollae tubus glaberrimus 11–12$^{\mathrm{mm}}$ longus, lobis ellipticis 2$^{\mathrm{mm}}$ longis. Antherae inclusae vix 2$^{\mathrm{mm}}$ longae. Ovarium calyce dimidio brevius, stylo ramis 2$^{\mathrm{mm}}$ longis computatis 7$^{\mathrm{mm}}$ longo, ovulis linearibus. Drupa desideratur.—Ob folia *C. filipedi* Benth. valde affinis differt praesertim pedunculis perbrevibus.

Ad ripas fluminis Ogewaj prope Sasís, Depart. Alta Verapaz, Guatemala, alt. 900$^{\mathrm{m}}$, Maj. 1908, *H. von Tuerckheim* (n. II. 2253).

Satyria meiantha Donn. Sm.—Folia juniora lanceolato-oblonga tenuiter acuminata basi acuta, provectiora ovalia bis longiora quam latiora utrinque subaequaliter angustata praetermisso utroque nervulo basali mox evanido triplinervia. Corymbi sessiles subsimplices, floribus minimis. Antherae tubo filamentorum paulo longiores apice acutae.

Frutex grandis congeneribus habitu similis. Folia in ramulis annotinis 13–17$^{\mathrm{cm}}$ longa 4.5–6$^{\mathrm{cm}}$ lata, in ligno vetere 18–19$^{\mathrm{cm}}$ longa 9$^{\mathrm{cm}}$ lata, nervis lateralibus utrinsecus 5–7, petiolis 1–1.5$^{\mathrm{cm}}$ longis. Corymbi ad nodos defoliatos 2.5–3$^{\mathrm{cm}}$ longi 8–14-flori, axibus confertis plerumque simplicibus 1$^{\mathrm{cm}}$ longis, bracteolis lanceolato-ovatis, basalibus 2$^{\mathrm{mm}}$ longis, medialibus 2 suboppositis 1$^{\mathrm{mm}}$ longis. Calycis tubus 1.5$^{\mathrm{mm}}$ longus 2$^{\mathrm{mm}}$-diametralis basi intrusus, limbus dentatus 1$^{\mathrm{mm}}$ altus. Corolla 11–12$^{\mathrm{mm}}$ longa etiam in sicco laete rosea minutissime puberula, lobis ovatis apiculatis membrana connexis. Stamina 5.5–6$^{\mathrm{mm}}$ longa, filamentorum tubo 2.5–3$^{\mathrm{mm}}$ longo, antheris majoribus 3–3.5$^{\mathrm{mm}}$ longis, omnium tubis sursum dilatatis apice acuto discretis, poris oblongo-ellipticis. Stylus paulo exsertus. Baccae deficiunt.

In silva montana prope Cobán, Depart. Alta Verapaz, Guatemala, alt. 1600$^{\mathrm{m}}$, Jan. 1908, *H. von Tuerckheim* (n. II. 2101).

Gonolobus (§MONOSTEMMA K. Schum.) **patalensis** Donn. Sm.—Folia oblongo-ovata acuminata leviter cordata sparsim minuteque strigillosa. Flores umbellatim cymosi. Corolla calyce 3-plo longior intus glabra colorato-reticulata lobis ovato-oblongis alte fissa. Corona cyathiformis gynostegium subincludens ab eo libera squamulis minutissimis bifidis 5-denticulata intus infra marginem squamula minuta cum marginalibus alternante instructa.

Suffrutex volubilis, ramis petiolis cymis calyce patenter pilosis. Folia 7–11$^{\mathrm{cm}}$ longa 3·5–6$^{\mathrm{cm}}$ lata, sinu aperto acuto, nervis lateralibus utrinque 5–6, petiolis 15–30$^{\mathrm{mm}}$ longis. Pedunculus 10–13$^{\mathrm{mm}}$ longus, pedicellis plerumque 5-nis 15–20$^{\mathrm{mm}}$ longis. Calycis partiti segmenta lineari-lanceolata 5$^{\mathrm{mm}}$ longa. Corolla 14$^{\mathrm{mm}}$ longa rotata extus pilis raris aspersa, lobis 10$^{\mathrm{mm}}$ longis obtusis. Corona 2$^{\mathrm{mm}}$ alta 3$^{\mathrm{mm}}$ lata. Pollinia pendula obovata. Folliculi ignoti.—Secundum conspectum a cl. *Schumann* ad coronam ordinatum gregi "Bb" ascribendus.

Patal, Depart. Baja Verapaz, Guatemala, alt. 1600$^{\mathrm{m}}$, Jul. 1908, *H. von Tuerckheim* (n. II. 2371).

Gonolobus (§MONOSTEMMA K. Schum.) **araneosus** Donn. Sm.—Folia oblongo- vel lanceolato-ovata acuminata leviter cordata molliter pilosa. Cymae umbelliformes petiolum paulo superantes, floribus inter minimos. Corolla calyce dimidio longior colorato-reticulata usque ad medium lobata intus praeter lobos triangulari-ovatos glabros niveo-arachnoidea. Corona cyathiformis gynophorum aequans ab eo libera callis bipartitis 5-denticulata, squamula interna minuta cum callis alternante.

Suffrutex volubilis, ramis petiolis cymis calyce patenter pilosis. Folia juniora sericea lineari-lanceolata, provectiora 6–8$^{\mathrm{cm}}$ longa 2·5–3·5$^{\mathrm{cm}}$ lata, sinu aperto acuto, nervis lateralibus utrinque 4–5, petiolis 10–20$^{\mathrm{mm}}$ longis. Pedunculus 3–5$^{\mathrm{mm}}$ longus, pedicellis 4–5-nis 3–7$^{\mathrm{mm}}$ longis. Calycis partiti segmenta lineari-lanceolata 5$^{\mathrm{mm}}$ longa. Corolla 8$^{\mathrm{mm}}$ longa rotata, lobis 4–4·5$^{\mathrm{mm}}$ longis acutis extus parce pilosiusculis apice ciliatis. Corona 1$^{\mathrm{mm}}$ alta 2$^{\mathrm{mm}}$ lata. Pollinia pendula compresso-orbicularia. Folliculi desiderantur.—Ad speciem praecedentem foliis calyce corona arcte accedens inflorescentia atque corolla insigniter recedit.

In montibus inter Tactic et Cobán, Depart. Alta Verapaz, Guatemala, alt. 1650$^{\mathrm{m}}$, Jul. 1908, *H. von Tuerckheim* (n. II. 2332).

Merinthopodium campanulatum Donn. Sm.—Pedicelli filiformes floribus permagnis paulo breviores. Corolla sepalis bis fere longior e fundo subcylindrico abrupte lateque dilatata, lobis elongato-triangularibus, sinubus acutis.

Epiphytale, foliis coriaceis ovalibus acutis (ex cl. repertore in literis). Pedicelli 6·5–8$^{\mathrm{cm}}$ longi. Sepala acutissima apiculata 5·1–5·3$^{\mathrm{cm}}$ longa basi 1·6–1·7$^{\mathrm{cm}}$ lata. Corollae virescentis in toto 10$^{\mathrm{cm}}$ longae pars tubiformis 2·6$^{\mathrm{cm}}$ longa, pars campaniformis 5·2$^{\mathrm{cm}}$ longa in sicco tam lata quam longa, lobi 2·2$^{\mathrm{cm}}$ longi, sinubus obsolete plicatis. Antherae 1·7$^{\mathrm{cm}}$ longae. Stylus 8$^{\mathrm{cm}}$ longus.

Quanquam folia non vidi, tamen ob flores ab eis *M. neuranthi* Donn. Sm. optime discrepantes plantam publici juris faciendam puto.

In silvis primaevis superioribus montis haud procul a Cobán, Depart. Alta Verapaz, alt. 1600$^{\mathrm{m}}$, Mart. 1908, *H. von Tuerckheim* (II. 2391).

Neotuerckheimia Donn. Sm., nov. gen. BIGNONIACEARUM e tribu CRESCENTIEARUM.—Calyx coriaceus glaber primum clausus denique in lobos 2 ovales inaequaliter ruptus. Corolla infra medium tubuloso-campanulata medio antice ad plicam transversam deorsum flexam geniculata ventricosa, limbo obliquo vix lobato crispatim dentato. Stamina 4 didynima inclusa paulo supra basin corollae inserta, loculis oblongis pendulis. Discus pulvinatus. Ovarium conicum costis 8 angulatum perfecte uniloculare, placentis 2 parietalibus valde intrusis, ovulis pluriserialibus, stylo angulato, stigmate bilamoso.—Arbores glabrae. Folia singula vel 3-fasciculata oblanceolata subsessilia. Nodi floriferi laterales vel terminales bracteis numerosis obtecti, pedunculis 1–5-nis. Corollae tubus plurinervis, limbus colorato-reticulatus.

In honorem nominavi liberi baronis *H. von Tuerckheim* floram Guatemalensem ad cognoscendam viginti tres per annos collaboratoris amicissimi.

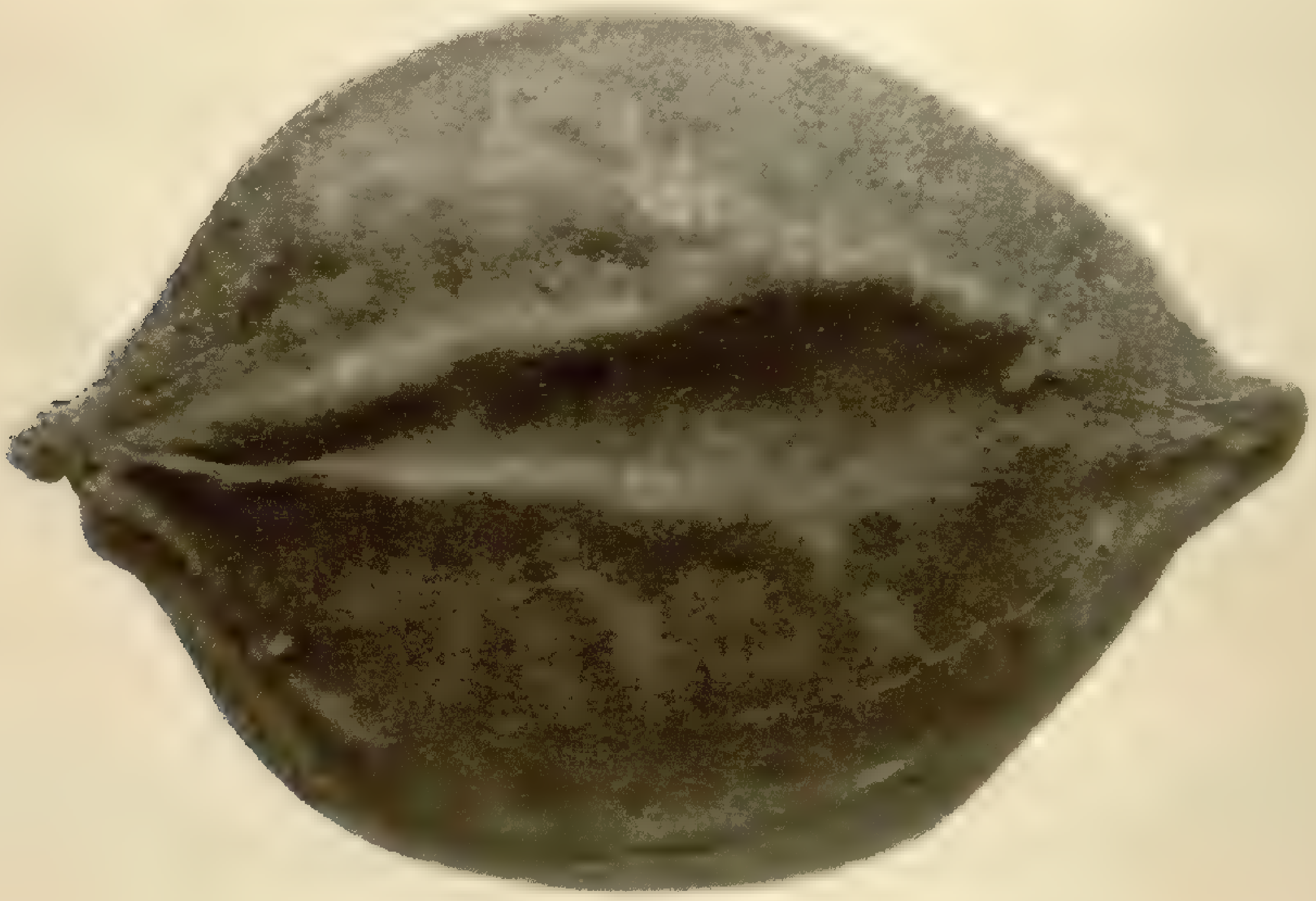

FIG. 1.—*Neotuerckheimia megalophylla; fructus.*

Neotuerckheimia megalophylla Donn. Sm.—Folia 3-fasciculata incurvo- et falcato-acuminata deorsum longissime attenuata. Pedunculi laterales squamis permultis cartilagineis circumdati solitarii vel bini. Corolla calyce dimidio longior, tubo angusto. Fructus ovoideus utrinque acuminatus octangularis.

Arbor 10-metralis cortice suberosa rimosa. Fasciculi foliorum juniorum oblanceolato-linearium 20–28^{cm} longorum ad apicem versus ramulorum arcte conferti. Folia provectiora usque ad 76^{cm} longa 11–13^{cm} lata chartacea diaphana, nervis lateralibus fortioribus utrinque 28–36, petiolis 6–8^{mm} longis tumidis corticatis. Nodi in ligno vetere floriferi squamis (seu bracteis pedunculos olim fulcientibus) concavis lanceolatis acutis armati, pedunculis 2–4^{cm} longis. Calyx 18^{mm} longus. Corolla 28^{mm} longa, plica retroflexa. Stamina 14–16^{mm} longa, loculis 4^{mm} longis. Discus 2^{mm} altus 3^{mm} latus. Ovarium 4^{mm} longum, stylo 13^{mm} longo. Fructus (*fig. 1*) nondum satis maturus 11^{cm} longus 7^{cm}-diametralis septis contrarie leviter compressus pericarpio cartilagineo tenui. Semina desunt.

Cubilquitz, Depart. Alta Verapaz, Guatemala, alt. 350^{m}, Sept. 1904, *H. von Tuerckheim*, n. 8723 ex Pl. Guat. etc. quas ed. Donn. Sm. Sub *Crescentia* olim distributa.—Ad ripas rivuli Chiú prope Cobán, Depart. Alta Verapaz, Guatemala, alt. 1350^{m}, Maj. 1908, *H. von Tuerckheim* (n. II. 2278).

Neotuerckheimia gonoclada Donn. Sm.—Folia singula cuspidato-acuminata deorsum attenuata. Pedunculi terminales 2–5-ni bracteis pluribus linearibus comitati. Corollae tubus late oblongus, limbus glanduloso-punctulatus.

Ramuli angulati, cortice exfoliato. Folia superiora approximata, inferiora internodiis 2–4^{cm} longis remota opaca 19–30^{cm} longa 5–7^{cm} lata, nervis lateralibus fortioribus utrinque 20–24, petiolis vix 2–3^{mm} longis crassis. Pedunculi 2.5–4^{cm} longi, bracteis 6–9^{mm} longis canaliculatis deciduis. Calyx 22^{mm} longus. Corolla 38^{mm} longa e schedula Tonduziana pallide flavicans, plica retroflexa 2.5^{mm} lata. Stamina 16–18^{mm} longa, loculis 4^{mm} longis. Discus 2^{mm} altus 4^{mm} latus. Ovarium 4^{mm} longum costis 8 angulatum, stylo 28^{mm} longo. Cetera desunt.

In silvis ad La Palma, Prov. San José, Costa Rica, alt. 1460^{m}, Sept. 1898, *Ad. Tonduz*, n. 7384 ex Pl. Guat. etc., quas ed. Donn. Sm. (n. 12563 herb. nat. Cost.). Sub *Crescentia* olim distributa.

Justicia (§TYLOGLOSSA Lindau) **multicaulis** Donn. Sm.—Folia inter minora rhomboideo- vel oblongo-ovalia vel lanceolata utrinque acuta. Flores axillares sessiles singuli vel subterminales et 2–4-ni interdum breviter spicati. Corollae tubus cylindricus limbo ampliato dimidio longior. Antherarum loculus inferior ab altero remotus appendicula ovali herbacea munitus.

Suffrutex nanus, caulibus e basi pluribus 25–33^{cm} longis, ramis herbaceis tetragonis bifariam pubescentibus lineolatis. Folia plerumque 15–32^{mm} longa 11–17^{mm} lata, interdum 34^{mm} longa 7^{mm} lata, cystolithis farcta praeter nervos subtus puberulos glabra, nervis laterlibus utrinque 4–5, petiolis bifariam puberulis 3–6^{mm} longis. Bracteae spatulato-obovatae 7^{mm} longae cum bracteolis lineari-spatulatis 5^{mm} longis herbaceae glabrae lineolatae. Calycis segmenta 5 linearia acuta 7^{mm} longa. Corolla 16^{mm} longa alba, tubo gracile 10^{mm} longo curvato, labio postico bidentato violaceo utrinque pubescente, antici paulo longioris lobis obovatis, intermedio maximo 4^{mm} longo atque lato. Stamina summis faucibus affixa 6^{mm} longa, antherarum loculo altero usque ad 0.5^{mm} inferius affixo perfecto.

Capsula oblonga acuminata 6^{mm} longa abortu disperma, retinaculis acutis, seminibus disciformibus rugosis alato-marginatis.—Corollae indole anormalis.

Ad ripas rivuli, Pansamalá, Depart. Alta Verapaz, Guatemala, alt. 1250^{m}, Jun. 1885, *H. von Tuerckheim*, n. 741 ex Pl. Guat. etc., quas ed. Donn. Sm. In silva montana prope Cobán, Depart. Alta Verapaz, Guatemala, alt. 1600^{m}, Jan. 1908, *H. von Tuerckheim* (n. II. 2091).

Ruprechtia (§PSEUDOTRIPLARIS Benth.) **Kellermanii** Donn. Sm.—Folia subsessilia elliptica acuminata basi obtusiuscula subglabra minute inconspicueque reticulata. Racemi fasciculati, bracteis pedicellos superantibus. Perianthium fructiferum inter minora totum cinereo-atque-cano-sericeum, segmentis exterioribus linearibus, interioribus dimidio adnatis. Achenium substipitatum tenuiter elongato-conoidale.

Folia coriacea $11–13.5^{cm}$ longa medio $5.5–6^{cm}$ lata, venulis retiformibus tantum ope lentis manifestis et puberulis, petiolis vix 2^{mm} longis. Racemi fructiferi densiflori pilosi, rhachi $1.5–3.5^{cm}$ longa, bracteis orbiculari- vel oblongo-ovatis $5–6^{mm}$ longis fuscis puberulis, pedicellis 4^{mm} longis cano-pilosis prope apicem articulatis. Perianthii $18–21^{mm}$ longi tubus oblongus $7–9^{mm}$ longus, segmenta exteriora apice 3^{mm} basi 2^{mm} lata obscure trinervia et reticulata, interiorum pars libera 3^{mm} longa. Discus staminum sterilium 1^{mm} altus 9-denticulatus. Achenium 9^{mm} longum 2.5^{mm} latum in imam basin stipitiformem 1^{mm} longam angustatum prope apicem acute triquetrum et ciliatum ceteroquin rotundato-trilobum, lobis sulcatis glabris, stylis 1^{mm} longis stigmata aequantibus. Cetera desunt.—*R. Deamii* Robinson ejusdem loci incolae valde affinis.—Beato KELLERMANI[1] florae Guatemalensis exploratori indefesso dicata.

Gualán, Depart. Zacapa, Guatemala, alt 122^{m}, Dec. 1905, *W. A. Kellerman* n. 5985.—Typus in herb. Musei Nationalis servatur.

SPECIEM AMERICAE AUSTRALIS INCOLAM LICEAT HIC ADJUNGERE

Ruprechtia (§PSEUDOTRIPLARIS Benth.) **colorata** Donn. Sm.—Folia oblongo-ovata vel -ovalia apice acuta vel obtusiuscula basi rotundata vel obtusa glabra subtiliter reticulata. Racemi singuli, pedicellis gracillimis. Perianthium fructiferum rubiginosum, segmentis exterioribus lineari-spatulatis glabrescentibus, interioribus liberis. Achenium lanceolatum acuminatum basi obtusum.

Arbuscula biorgyalis. Folia coriacea $8.5–12^{cm}$ longa $4–4.5^{cm}$ lata, venulis retiformibus non nisi oculo armato perspicuis, petiolis $3–4^{mm}$ longis. Racemi fructiferi solum visi sublaxiflori pubescentes, rhachi $2–4^{cm}$ longa, bracteis ocreatis apice ovatis $1.5–2^{mm}$ longis, pedicellis $5–7^{mm}$ longis medio articulatis. Peri-

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[1] Obiit in Guatemala m. Mart. ann. 1908 febri confectus.

anthii 27–29$^{\mathrm{mm}}$ longi tubus obovatus 5–6$^{\mathrm{mm}}$ longus pubescens, segmenta exteriora apice 5$^{\mathrm{mm}}$ basi 2$^{\mathrm{mm}}$ lata pulchre trinervia et reticulata, interiora 4$^{\mathrm{mm}}$ longa. Discus staminum sterilium 0.5$^{\mathrm{mm}}$ altus 9-denticulatus. Achenium glabrescens 9$^{\mathrm{mm}}$ longum 3$^{\mathrm{mm}}$ latum triente superiore acute triquetrum inferne rotundato-trilobum, lobis leviter sulcatis, stigmatibus 2$^{\mathrm{mm}}$ longis stylos 3-plo superantibus. —*R. fuscae* Fernald et *R. Cumingii* Meisn. affinis perianthis etiam in sicco laete colorato insignis.

In collibus sabulosis prope litora oceani, Savanilla, Republica Colombiana, Febr. 1896, *J. Donnell Smith.*

Daphnopsis (§Nordmannia Benth. et Hook.) **monocephala** Donn. Sm.—Folia sessilia oblanceolata apice rotundata infra medium sensim attenuata supra glabrescentia subtus cano-sericea. Pedunculus subterminalis solitarius simplex gracilis cum capitulo unico cano-sericeus. Perianthium masculinum subsessile anguste infundibuliforme, lobis obtuse ovatis tubo 3-plo brevioribus intus glabris, squamulis 4 ovalibus.

Rami dichotomi ad apicem versus cano-villosi et confertim foliacei. Folia juniora utrinque villosa, provectiora (saltem superiora) 5–6.5$^{\mathrm{cm}}$ longa 1.5–2$^{\mathrm{cm}}$ lata coriacea, nervis lateralibus utrinsecus 5–6 longe ascendentibus et reticulis subtus prominulis, areolis pellucidis. Pedunculus infra gemmam apicalem ortus circiter 2$^{\mathrm{cm}}$ longus vel interdum abortu 5–7$^{\mathrm{mm}}$ longus, receptaculo convexo 3$^{\mathrm{mm}}$ lato 30–40-floro, pedicellis persistentibus obconicis circiter 1$^{\mathrm{mm}}$ longis. Perianthii masculini tubus 4.5$^{\mathrm{mm}}$ longus ore 1.5$^{\mathrm{mm}}$ latus, squamulis hypogenis rudimento pistilli glabro triplo brevioribus. Perianthium femininum ignotum.

El Rancho, Depart. Baja Verapaz, Guatemala, Jan. 1906, *W. A. Kellerman* n. 5714.—Typum in herb. Musei Nationalis vidi.

Euphorbia (§Alectoroctonum Boiss.) **adinophylla** Donn. Sm.—Glabra. Folia in quoque verticillo indefinite compluria rhomboideo-elliptica apice obtusa vel rotundata basi acuta petiolos subaequantia. Cymae axillares et terminales corymbiformes petiolis subaequilongae. Involucrum graciliter pedicellatum, glandulis 5 appendice subcrenulata paulo angustioribus. Styli brevissime lobulati.

Fruticosa, ramis verticillatis sulcatis, internodiis 5–9$^{\mathrm{cm}}$ longis. Folia 6–16-verticillata 25–33$^{\mathrm{mm}}$ longa 14–18$^{\mathrm{mm}}$ lata, petiolis filiformibus 20–37$^{\mathrm{mm}}$ longis. Cymae obpyramidatae pedunculo 5–7$^{\mathrm{mm}}$ longo computato 22–36$^{\mathrm{mm}}$ longae 30–35$^{\mathrm{mm}}$ latae repetitus dichotomae, foliis floralibus oblanceolatis 3–7$^{\mathrm{mm}}$ longis, dichotomiis glandula magna instructis, axibus uti pedicelli 2–5$^{\mathrm{mm}}$ longi sulcatis. Involucri tubus campanularis 1.5–2$^{\mathrm{mm}}$ longus inferne sulcatus, lobi minuti obovati fimbriati, glandulae transverse ellipticae ab appendice arcuata margine liberae. Ovarium longe stipitatum, stylis indivisis 1.5$^{\mathrm{mm}}$ longis. Capsula ignota.—Ab *E. Schlechtendalii* Boiss. proxima differt foliis pro rata longioribus ad nodos confertioribus, inflorescentia evoluta, pedicellis elongatis, stylis indivisis.—Ab incolis *Caraña* (Latine *Resina*) vocatur.

Republica El Salvador, loco natali haud accuratius addicto, ann. 1905, *Cárlos Rénson* (n. 187).—Typus in herb. Musei Nationalis servatur.

GUZMANIA BRACTEOSA André.—Folia auctoribus adhuc ignota linearia 30–55^{cm} longa acute attenuata medio 13–25^{mm} lata in vaginam 25–50^{mm} latam sensim dilatata tenuiter coriacea utrinque praesertim subtus pallide lepidota vel glabrescentia, nervis crebris utrinque prominentibus.

In silvis ad Las Vueltas, Tucurrique, Costa Rica, alt. 635^{m}, Mart. 1899, *Ad. Tonduz* (n. 13291).—Epiphyta (ex cl. repertore) in silvis montanis prope Purulá, Depart. Baja Verapaz, Guatemala, alt. 1800^{m}, Apr. 1907, *H. von Tuerckheim* (n. II. 1826).

BALTIMORE, MARYLAND

COMPARATIVE HISTOLOGY OF FRUITS AND SEEDS OF CERTAIN SPECIES OF CUCURBITACEAE

KATE G. BARBER

(WITH FIFTY-THREE FIGURES)

Introduction

This investigation was undertaken with the view to supplementing the work already done on the histology of the fruits and seeds of Cucurbitaceae. The literature, although not meager, treats only of the most conspicuous elements of the spermoderm, ignoring, with a few exceptions, the less important tissues of the seed and the whole of the pericarp.

In the following paper are included additions to the histology of the spermoderm and new descriptions of the pericarps of the common species; also brief descriptions of six interesting seeds previously undescribed.

I wish to acknowledge my great indebtedness to Dr. A. L. WINTON, under whose guidance and inspiration this work was carried on, and also to Professor A. W. EVANS for advice in its preparation.

Résumé of the literature

In 1833 BISCHOFF[1] published two cuts showing cross-sections of the seed coats of *Cucurbita Pepo* and *C. Lagenaria*, which, according to FICKEL,[2] leave much to be desired with regard to detail.

VON HÖHNEL[3] was the first to publish a detailed description of the seed coats of the Cucurbitaceae, the species studied being *Cucurbita Pepo* L., *Lagenaria vulgaris* Ser., and *Cucumis sativus* L.

A thorough investigation of the integuments, from before fertilization of the flower until maturity, led him to conclude that: (1) the inner integument (three to four layers thick) develops but slightly, becoming the collapsed, thin-walled inner parenchyma of the seed coat; and (2) the outer integument (eight to ten layers thick) forms the greatly differentiated outer layers of the coat.

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[1] Handbuch der bot. Terminologie und Systemkunde. *pl. 43. figs. 1872, 1873A.*

[2] Ueber die Anatomie und Entwickelungsgeschichte der Samenschalen einiger Cucurbitaceen. Bot. Zeit. **34**:738. 1876.

[3] Morphologische Untersuchungen über die Samenschalen der Cucurbitaceen und einiger verwandter Familien. Sitzb. Akad. Wiss. Wien, Mathem.-Naturw. **73**:297. 1876.

At maturity he found that the spermoderm consists of a complicated structure with five distinct tissues, namely: (1) inner epithelium of the carpel; (2) outer and (3) inner integument; (4) perisperm; and (5) endosperm. These five in turn are subdivided into ten layers, each one to many cells thick. About the edge of the seed, between the fifth and sixth layers, runs the small raphe.

This author divided the family into two large groups. In the first belong those seeds with the epithelium of the carpel firmly attached to the spermoderm, represented in his work by *Cucurbita Pepo* and *Lagenaria vulgaris*. The second includes the species without this epithelium, illustrated by *Cucumis sativus*. Otherwise there are no great differences in development.

In the same year, one month after the appearance of VON HÖHNEL's paper, FICKEL[2] published his inaugural dissertation, describing the seed coats of *Cucumis sativus* L., *C. Dudaim* L., *C. myriocarpus* Naud., *Cucurbita Pepo* L., *C. melanosperma* A. Br., *Lagenaria vulgaris* Ser., *Citrullus vulgaris* Schrad., *Benincasa cerifera* Savi., *Bryonia alba* L., *B. dioica* L., *Ecballium agreste* Rchb., *Sicyos angulatus* L., *Cyclanthera explodens* L., *C. pedata* Schrad., and *Bryonopsis erythrocarpa*. He gives descriptions and cuts of the mature seed coat and its development from the two integuments, and reaches the following conclusions: (1) the seed coat has five layers; (2) the epidermal cells are radially elongated and, with the exception of those of Sicyos and Cyclanthera, have thickenings of various kinds on the radial walls; (3) the second layer consists of one or more layers of cells varying in size and thickness of walls; (4) a third layer has either radially or longitudinally elongated cells; and (5) the remaining layers are of compressed cells without definite structure.

GODFRIN[4] briefly notes the seed coats of *Cucumis sativus* L., *Cucurbita maxima* Duch., *Lagenaria vulgaris* Ser., *Sicyos angulatus* L., and *Cyclanthera pedata* Schrad. In his general description the spermoderm is represented as having six layers, as follows: (1) epidermis of prismatic cells; (2) small cells differing as to number, size, and

[4] Etude histologique sur les téguments séminaux des angiospermes. Soc. Sci. Nancy **1880**:160.

thickness of walls; (3) a single layer of sclerenchymatized cells varying but slightly in all the species; (4) outer and inner parenchyma; (5) inner epidermal cells, often separated from the preceding layer by longitudinally elongated cells; and (6) inner row of thick-walled cells with granular contents, the author evidently including the endosperm in the spermoderm. This is followed by a description of each of the species already mentioned.

VON HÖHNEL'S division of the family into two groups, distinguished by the presence or absence on the spermoderm of the inner carpellary layer, is criticized, as GODFRIN always found this layer present in fresh material. He used the following grouping, based on the elongation of the cells of the "protective" (third) layer: (1) tangentially elongated cells (Cucumis, Lagenaria, Cucurbita, Citrullus); and (2) radially elongated cells (Sicyos and Cyclanthera). The individual descriptions are brief, many details being omitted.

FISCHER[5], in his classical work on sieve tubes of the Cucurbitaceae, describes a detailed study of the elements in all parts of the plant. The tubes are of four kinds: (1) bundle sieve tubes (usual type found in fibro-vascular bundle); (2) ectocyclic (isolated tubes of hypoderm); (3) entocyclic (isolated tubes of the inner tissues); and (4) commisural (connecting those of the bundle with the isolated tubes). In the young isolated tubes the contents are thickened but in the old there is a watery slime secreted by the neighboring cells. These isolated tubes, being free from callus plates, were mistaken by earlier writers for latex tubes.

Six plates are given illustrating these tubes in *Cucurbita Pepo*, *Lagenaria vulgaris*, *Sicyos angulatus*, *Cyclanthera pedata*, *Melothria pendula*, *Bryonia alba*, and *Luffa pentandra*.

T. F. HANAUSEK[6] gives chemical analyses of *Cucumis sativus* L., *C. Melo* L., *C. Citrullus* L., *Cucurbita Pepo* L., and *C. maxima* Duch., and mentions briefly the histology of each.

HARZ[7] describes and illustrates cross-sections of species of Cucumis, Citrullus, Lagenaria, and Cucurbita. The numerous species are divided into races, varieties, and subvarieties, with long lists of synonyms under each. The author briefly notes the macroscopic appearance of the fruit, then gives short histological descriptions of the seed. According to his division the spermoderm has five layers. Some of the details of structure of the outer layers, and nearly all of the inner ones, are omitted.

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[5] Untersuchungen über das Siebröhren-System der Cucurbitaceen. Berlin. 1884.

[6] Die Nahrungs- und Genussmittel aus dem Pflanzenreiche 195. Kassel. 1884.

[7] Landwirthschaftliche Samenkunde 767. Berlin. 1885.

VOGL[8] devotes but a single paragraph to a microscopical description of Cucurbitae.

BRAEMER[9] in 1893 studied the stem, leaf, pericarp, and seed of *Bryonia dioica* Jacq., *Ecballium Elaterium* Rich., and *Citrullus Colocynthis* Schrad., but confined his attention chiefly to a microchemical investigation of the contents of the sieve tubes and latex tubes, both of which he regards as latex tubes, accepting the descriptions of the tissues given by earlier writers. According to his introduction, the pericarp has an outer and inner epidermis with a sarcocarp between. Within the spermoderm, having hard and lignified layers, are inclosed an embryo, reduced to a small radicle and two cotyledons, rich in oil and aleurone grains, and the remains of the perisperm and endosperm.

The main part of the paper is devoted to the long, ramifying, straight or sinuous tubes containing a yellow semi-fluid, finely granular, refractive substance which entirely fills the cavity. Both lateral and cross walls are composed of cellulose without any indications of sieve or callus plates. In their morphological and chemical characters they resemble the latex tubes of Convolvulaceae and Campanulaceae, and the isolated sieve tubes of FISCHER. In these tubes BRAEMER found the three "active principles" bryonin, colocynthin, and elaterin.

PLANCHON and COLLIN[10] treat the species used as drugs. Macroscopic and microscopic sections are figured, but no histological details are given, of the fruits and seeds of *Cucurbita Pepo* Duch., *Citrullus Colocynthis* Schrad., *Cucumis sativus* L., *Ecballium Elaterium* Rich., and Fevileae.

VILLIERS and COLLIN[11] use the bicollateral bundles and sieve tubes (or latex tubes) in the detection of pumpkin pulp as an adulterant of preserves. They have an original cut, but their description of these elements is taken from FISCHER[5] and BRAEMER.[9]

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[8] Pharmakognosie 196. Wien. 1892.

[9] De la localisation des principes actifs des Cucurbitacées. Toulouse. 1893.

[10] Les drogues simples d'origine végétale 2:292. Paris. 1896.

[11] Traité des altérations et falsifications des substances alimentaires 454. Paris. 1900.

T. F. HANAUSEK[12] gives one figure illustrating the characteristic elements of the seed of *Cucurbita Pepo* L., *C. maxima* Duch., and *C. moschata* Duch. These elements are the *Skleriden* (resembling the epidermis of Spanish pepper), spongy parenchyma, starch grains of the inner parenchyma, endosperm and cotyledon tissue with aleurone grains.

ARTHUR MEYER[13] refers briefly to the aleurone grains of *Cucurbita Pepo* as having a diameter of 1–4 μ (mostly 3 μ) and small crystalloids. In his table taken from LUDTKE,[14] the seeds of Citrullus and Colocynthis are stated to contain numerous aleurone grains 1–7.5 μ in diameter, each having one globoid (0.5–1 μ) and one crystalloid (1–3 μ).

BÖHMER[15] gives a chemical analysis of the seeds of the Cucurbitae and one figure showing a cross-section and surface view. His brief histological description is taken from other authors.

COLLIN and PERROT[16] describe briefly and give a cross-section of the seed of *Cucurbita Pepo* Duch.

According to MOELLER[17] the fruits of Cucurbitaceae are all large berries with hard shells, soft fruit-flesh, and many seeds. The seed coat is divided into four tissues: (1) palisade cells with thickenings on radial walls; (2) stone-cell layer; (3) stellate parenchyma; and (4) thin-walled parenchyma. A brief description follows of *Cucurbita Pepo* L., *C. maxima* Duch., *C. moschata* Duch., *Cucumis sativus* L., *C. Melo* L., and *Citrullus vulgaris* Schrad., with cuts of the last two.

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[12] Lehrbuch der technischen Mikroskopie 370. Stuttgart. 1901. Translation, WINTON, The microscopy of technical products 369. New York. 1907.

[13] Die Grundlagen und die Methoden für die mikroskopische Untersuchung von Pflanzenpulvern 32. Jena. 1901.

[14] Ueber die Beschaffenheit der Aleuronkörner einiger Samen. Ber. Deutsch. Pharm. Gesells. **1891**: 56–59.

[15] Die Kraftfuttermittel, ihre Rohstoffe, Herstellung, Zusammensetzung, Verdaulichkeit und Verwendung, mit besonderen Berücksichtigung der Verfälschungen und der mikroskopischen Untersuchung 508. Berlin. 1903.

[16] Les résidues industriels 270. Paris. 1904.

[17] Mikroskopie der Nahrungs- und Genussmittel 470. 2. Aufl. Berlin. 1905.

BARBER,[18] in a chapter on Cucurbitaceae, gives brief descriptions of *Cucurbita Pepo* L., *C. maxima* Duch., *Cucumis sativus* L., *C. Melo* L., and *Citrullus vulgaris* Schrad., illustrating the first-named species by three original cuts.

Geographical distribution

The Cucurbitaceae are scattered over the greater part of the earth's surface, but reach their highest development in the tropics. Representatives are, for the most part, absent in the colder regions of the temperate zone, the two exceptions being *Sicyos angulatus*, found in Canada, and *Echinocystis lobata* in New England.

The total number[19] of genera is eighty-five, the Old World claiming fifty-four and the western hemisphere thirty-eight, while seven are common to both. Under each there are long lists of species, subspecies, and varieties, authors differing greatly as to the number.

EDIBLE SPECIES.—Many species have long been cultivated for food. Probably one of the oldest on record is Citrullus (watermelon), a favorite with the ancient Egyptians. Other important species are *Cucumis sativus* (cucumber), eaten in China as a vegetable more than two centuries before the Christian era; *Cucurbita Pepo* (pumpkin), grown by the aborigines in America; and *Cucumis Melo* (musk melon), greatly prized in Asia and Africa. These have now spread to all the warmer regions of the earth.

ORNAMENTAL SPECIES.—There are many varieties grown for the curious form and vivid coloring of the fruit, among which are *Momordica balsamina* (balsam apple), *Lagenaria vulgaris* Ser. (common gourd), *Cucumis erinaceus* (hedge-hog gourd), *Cyclanthera explodens* (squirting cucumber), and *Luffa cylindrica* (dish-cloth gourd).

PHARMACEUTICAL SPECIES.—Among those used for drugs, both here and in Europe, are *Bryonia dioica* (bryony), *Citrullus Colocynthis* (colocynth), and *Ecballium Elaterium* (elaterin).

General characters

MACROSCOPIC

FLOWER.—The axillary flowers, yellow or white in color, are borne either solitary or in groups of various kinds. They are usually monoecious, epigynous; calyx and corolla actinomorphic, adnate at the base. The stamens are five in number, four of which frequently cohere in pairs, or more rarely they all unite to form a column. The ovary is one- to five-, usually three-celled.

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[18] In WINTON, Microscopy of vegetable foods 401. New York. 1906.

[19] ENGLER UND PRANTL, Pflanzenfamilien IV. 5:9.

FRUIT.—In the Cucurbitaceae are found the largest fruits of the whole plant kingdom. From the enormous berry of Cucurbita, reaching a maximum of several kilos in weight, there are all gradations down to the small burr of *Sicyos angulatus*, only slightly larger than the single inclosed seed.

The fruits are nearly always fleshy berries; they may, however, become membranaceous and dry, preserving at the same time their original shape. There is no characteristic form for the family, the shape differing as much as the size. All possible variations of spherical, elliptical, greatly elongated, and curious unsymmetrical forms are represented. They are smooth, warty, or covered with spines, or various other kinds of emergences. In addition to these outgrowths, the young fruits of all the common species bear one or more forms of hairs which, in most cases, persist at maturity. The color varies from white, green, and yellow to red, with spots and stripes on some of the varieties.

All the fruits described in this paper are indehiscent with the exception of Echinocystis, which bursts irregularly at the top.

The pericarp, or rather the pericarp and adherent receptacle, varies in thickness (thin or thick rind, or solid fruit-flesh), color (white, green, yellow, or red), and texture (watery or dry, sclerenchymatized or soft). The central placentae extend to the outer wall and divide, turning back so as to give a parietal appearance.

SEED.—The seeds, borne either singly or in great numbers, are anatropous, large, ovate, and flattened, with or without a border (formed by elongated epidermal cells) on each side at the edge. They vary in shape from the narrow and pointed to the broad, rounded, or rectangular forms, and in color from white to brown and black.

MICROSCOPIC

PERICARP.—The pericarp may be divided into six, more or less distinct tissues as follows:

1. *Epicarp.*—The cells are for the most part polygonal, forming

a palisade layer, those about the stomata being frequently elongated. The outer and radial walls are cuticularized and occasionally colored.

2. *Hypoderm.*—Few or many layers of isodiametric cells form the tissue beneath the epicarp. The cells are somewhat thickened and occasionally pitted.

3. *Outer mesocarp.*—Isodiametric cells with either cellulose, or sclerenchymatized and pitted, walls (stone cells, etc.) form a sharply defined zone varying from a few to many cells in thickness.

4. *The middle mesocarp* consists of large, usually isodiametric, thin-walled cells, often turgid with a watery cell sap and containing a small amount of starch. The starch grains are small, with an average diameter of 10 μ. They are truncated, frequently occurring in aggregates of two and three, with slightly eccentric hilum and faint rings. Polarization crosses are very distinct.

5. *Inner mesocarp.*—Several layers of thin-walled cells, forming this tissue, closely resemble the preceding layers. The cells are small and have no visible contents.

6. *Endocarp.*—Very small, thin-walled, tangentially elongated cells, arranged side by side in groups, form a thin transparent tissue. With the exception of Cucumis, this layer remains so firmly attached to the dry seed that some authors describe it as the outer layer of the spermoderm.

The anastomosing *bundles* occurring throughout the mesocarp are bicollateral. They are either small and soft, or large and stiff, forming a conspicuous network. The elements consist of spiral, annular, and reticulated vessels, and sieve tubes having large sieve plates evident without staining.

Isolated sieve tubes and latex tubes.[20]—FISCHER[5] claims there are no true latex tubes, those known by this name being simply sieve tubes that have ceased to function; BRAEMER[9] and other later authors, however, use the term "latex tubes." I have seen the perforated plates in some tubes and have not found them in those containing granular milky contents which harden in alcohol, therefore shall mention both in the following descriptions. These elements occur in considerable numbers throughout the middle tissues of the pericarp.

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[20] According to DE BARY (Comparative anatomy of the vegetative organs of the phanerogams and ferns 198. Oxford. 1884) DIPPEL finds the septa and lateral walls of articulated tubes provided with sieve plates and thinks them intermediate between sieve tubes and latex tubes. DE BARY himself finds not the plates but perforations scattered over the whole wall, and further states that there are two kinds of latex tubes which do not correspond in function: (1) those secreting tannin, etc., and (2) those (of milky plants) which are closely related to sieve tubes.

Each seed has a firm spermoderm of many layers, a thin collapsed perisperm and endosperm, and a large embryo consisting of two large, flat, leaf-like cotyledons and a small radicle.

SPERMODERM.—Authors variously state the number of layers in this leathery coat or shell as four[17] to ten.[21] I myself consider it as consisting of five distinct tissue layers, the second being occasionally differentiated into two, and the fourth often into two or three forms of cells arranged in as many layers. It is developed from the two integuments (*fig. 10*), the outer integument forming the three outer and part of the fourth layers, the remainder of the coat developing from the inner integument.

1. *The epidermis* consists of a single layer of prismatic palisade cells, polygonal in surface view. They are usually of equal height over the flat surface of the seed, increasing in height at or on both sides of the edge. The radial walls of a few species (as *Echinocystis lobata*) are uniformly thickened; in all the other seeds they have either straight or branched thickenings running from the inner to the outer tangential walls. The outer walls, and frequently the inner, are thickened.

VOGL,[8] the only author that notes the presence of starch in this layer, gives no description of the grains. According to my own observation they are small, globular, reaching a maximum diameter of 7 μ, the larger ones showing a central hilum but no rings. They polarize very indistinctly.

2. *Subepidermal layer.*—One or more layers of sclerenchymatized cells, varying greatly in size and shape, make up this layer. The cells are either small, pitted, without intercellular spaces (Cucurbita), or longitudinally elongated, arranged end to end in rows, with numerous characteristic intercellular spaces (Cucumis), or form a thick layer of greatly thickened irregularly arranged cells. No contents are evident.

3. *Sclerenchyma.*—This consists of a layer of exceedingly thick-

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[21] ENGLER UND PRANTL, Pflanzenfamilien IV. 5:8.

walled cells elongated either tangentially and arranged end to end in longitudinal rows, or radially forming a palisade layer. The walls are sinuous with numerous pits, and after maceration the margins of the outer and inner tangential walls are seen to be lobed, each lobe branching with the ends overlapping and fitting together to form a flat compact layer (*fig. 18*). The empty cell cavities are comparatively small and present a striking oval appearance in median section.

4. *Parenchyma.*—Many cell layers of spongy parenchyma, differing greatly in size and shape, make up this layer. The cells of the outer layers are usually small and frequently sclerenchymatized and pitted. Within these small cells are one or more layers of either large or small stellate cells having very large intercellular spaces. Their thin walls are usually sclerenchymatized and often pitted or reticulated (Cucurbita). The remaining layers consist of small, thin-walled spongy parenchyma cells containing chlorophyll in some species.

The small raphal bundles are found imbedded in this parenchyma usually about the edge only; a few exceptions, however, show branches on the flattened surface of the seed.

5. *Inner epidermis.*—A single layer of small, polygonal, and inconspicuous thin-walled cells forms the inner tissue.

PERISPERM.—This thin coat is collapsed in the mature fruit, but treatment with Javelle water brings to view several layers of small, very thin-walled cells covered with an epidermis having cuticularized outer and radial walls. No contents are evident.

ENDOSPERM.—This consists of one layer of very thick-walled polygonal cells, containing oil and protein granules. A few exceptions (as *Citrullus vulgaris*) have within this layer several more layers of empty thin-walled cells.

EMBRYO.—The leaf-like cotyledons have an epidermis of small cells below which, on the inner side, are two sharply defined palisade layers. Procambium bundles run through the small-celled mesophyll. All of the cells are filled with oil and protein granules containing globoids and crystalloids which are very minute and of practically no diagnostic importance.

Specific characters.

CUCURBITA PEPO L.

Cucurbita Pepo L. (pumpkin), according to the earlier writers, was introduced from southern Asia, but WITTMACK, in his recent investigations of prehistoric remains in Peru, claims it to be a native of America. Early explorers also recorded the cultivation of this fruit by the aborigines in their maize fields.

The fruit is one of the largest of the Cucurbitaceae, occasionally reaching a weight of 200 kilos. It is a smooth, apple-shaped berry, with about twenty, more or less pronounced, longitudinal grooves, the color varying from yellowish green to orange. There are many subspecies, differing greatly in size and shape, of which HARZ enumerates thirty. Among them are the small to enormously large spherical, ellipsoidal, flask-, egg-, J-, and curiously-shaped forms. Most of the larger ones are cultivated for food, the smaller as ornamental fruits.

At maturity the fruit consists of a hollow, yellow rind, 2–3$^{\mathrm{cm}}$ in thickness, containing a tangle of slimy fibers, among which are the numerous flattened seeds.

The white seeds (*fig. 1*) are 1.5–2.5$^{\mathrm{cm}}$ in length, elliptical, flattened, and have a narrow border about the edge on both sides.

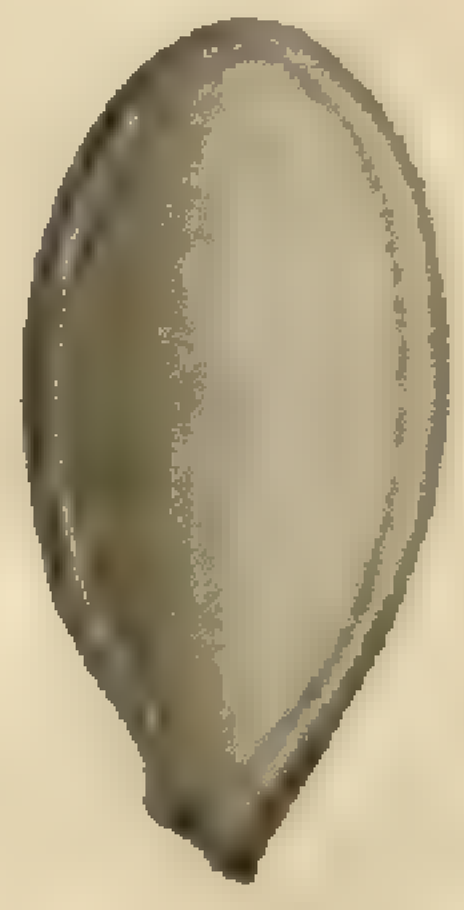


FIG. 1.—*Cucurbita Pepo* L. Seed. ×1.

PERICARP.—This makes up the bulk of the fruit. It includes the rind and fibers, the connecting parenchyma breaking down before the fruit reaches maturity.

1. *Epicarp* (*figs. 2, 3, epi*).—The prismatic cells form a palisade layer about 50μ in height, with outer and radial walls greatly thickened, cuticularized, and colored bright yellow. In surface view they are polygonal (14μ in diameter), except at characteristic white spots about which they are elongated and curved. These white spots consist of a stoma of the common type, from which radiate rows of tangentially elongated epidermal cells. The stomata are not uniformly distributed and occasionally two are found in the same group of radiating cells.

On the very young fruit, even before the fertilization of the ovary, two forms of hairs are found (*fig. 3*). Both arise from a foot-cell differing from the neighboring epidermal cells only in the more rounded shape. The hairs dry up and disappear while the fruit is still very small, leaving the foot-cell intact. Later the epidermal cells divide, thicken their walls, and press against the foot, which thus becomes polygonal. As both kinds of cells are of the same size, the two are indistinguishable, which accounts for the absence of hair scars on the mature fruit.

The first form of hair is jointed (t^1) and of great size, often reaching a length of 1.5–2^{mm}. The diameter increases rapidly (up to about 85 μ) for a short distance from the foot, then gradually tapers, forming a long, thick-walled (5 μ), conical hair. The first few cells are two or three times as broad as long, while the following cells become elongated as the hair increases in size.

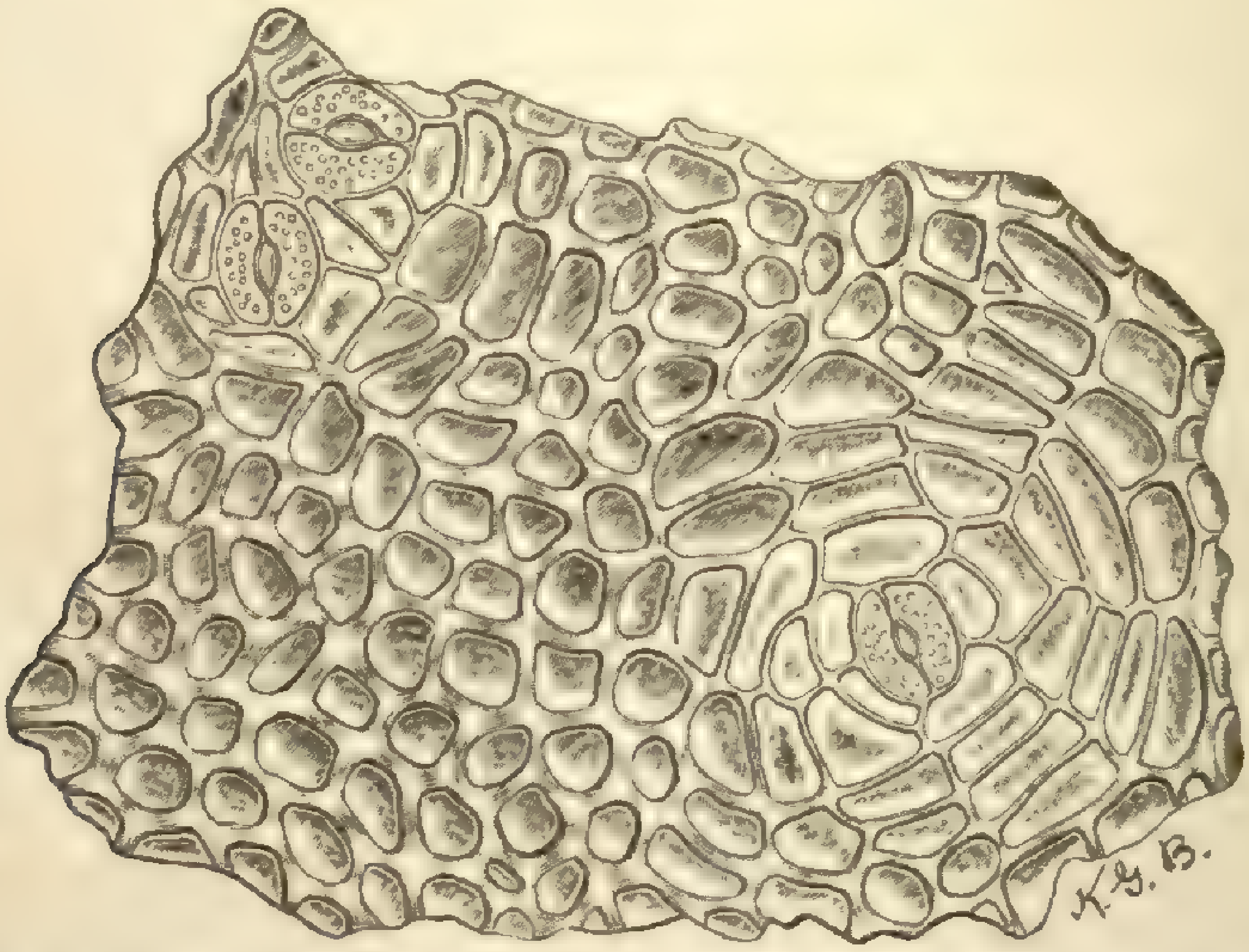


FIG. 2.—*Cucurbita Pepo* L. Epicarp in surface view. ×320.

The second form is capitate (t^2), and like the first increases in diameter from the foot, forming a jointed stalk of four or five cells. It ends with a large spherical head of one or more cells, often 54 μ in diameter.

2. *Hypoderm.*—Many cell layers of exceedingly small, isodiametric cells, 20 μ in diameter, form this layer. The cells have thick walls, occasional pits, and small intercellular spaces. The visible contents consist of numerous protein granules. This layer closely resembles the corresponding one of *C. Pepo* var. *verrucosa* Naud. (*fig. 7, hy*).

3. *Outer mesocarp.*—Within the preceding layer is a region composed of cells graduating in size from the small cells of the hypoderm

to the large ones of the middle mesocarp. They are isodiametric, have thick walls and intercellular spaces, and but few contents.

4. *Middle mesocarp* (*fig. 4*).—In this layer the cells become gradually larger, thicker-walled, and more loosely arranged. They contain small starch grains (*am*), reaching a maximum size of 10 μ. The outer cells contain a considerable number of these grains, but the increase in size of the cells is accompanied by a decrease in amount of starch.

5. *Inner mesocarp.*—This layer consists of rather large-celled parenchyma with no evident contents.

Bundles and isolated sieve tubes, together with anastomosing latex tubes (*lat*) are found throughout the mesocarp, while in the center of the fruit there is a great mass of tough fibers, surrounded by the remains of the broken-down parenchyma.

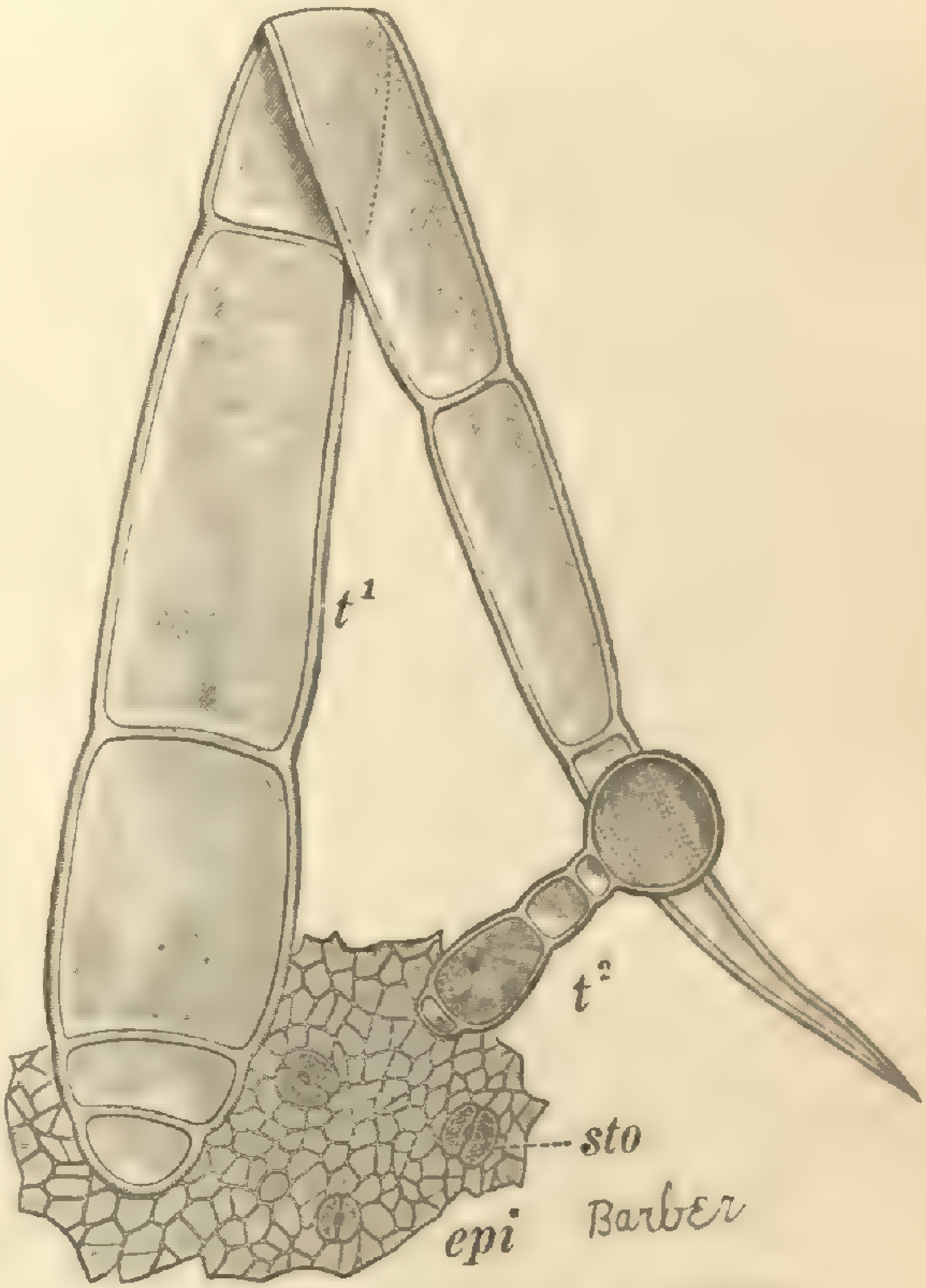


FIG. 3.—*Cucurbita Pepo* L. Immature epicarp in surface view; *epi*, epicarp with *t*¹, jointed conical hair, *t*², capitate hair, and *sto*, stoma. ×160.

6. The *endocarp* appears on the seeds as a thin membrane of longitudinally elongated cells, arranged end to end in rows. The inner wall is about the same thickness as the outer wall of the epidermis of the spermoderm, to which it is quite firmly attached; from the dry seeds, however, it may be readily separated as a thin, transparent, colorless skin.

SPERMODERM (*figs 5, 6*).—The five layers making up the spermoderm are as follows:

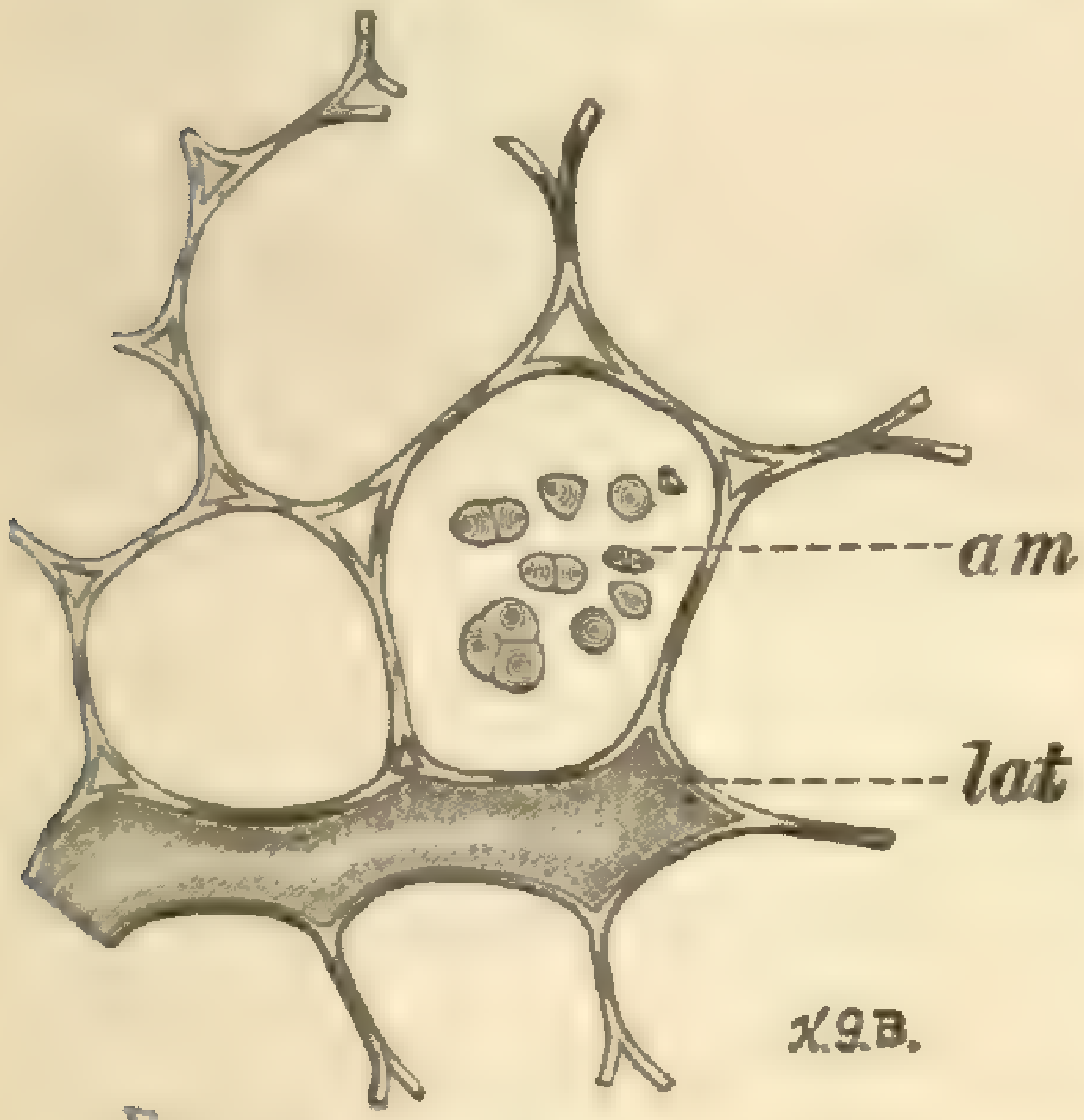


FIG. 4.—*Cucurbita Pepo* L. Cross-section of mesocarp showing *am*, starch grains, and *lat*, latex tube. ×160.

1. *Epidermis* (*ep*).—The prismatic cells form a continuous layer without intercellular spaces. They are radially elongated, on the flat side of the seed to 270 μ, on the edge to 50 μ, while the border consists of a ridge of cells several times as high as those of the flattened surface. The outer wall is thickened, but has no cuticle, and the radial walls are very thin, with peculiar branching thickenings of cellulose. The thickenings run from the base of the cell, one on each wall, as single straight rods until near the outer wall, where they branch profusely, giving rise to a beaded appearance in tangential section. After maceration, or in scrapings of the spermoderm, the rods fall upon their sides, presenting the appearance shown in *fig. 5*, ep^{1}. In dry seeds the walls of this layer are frequently broken down, and only a few of the thickenings remain, which may be mistaken for the cut surface of the walls themselves.

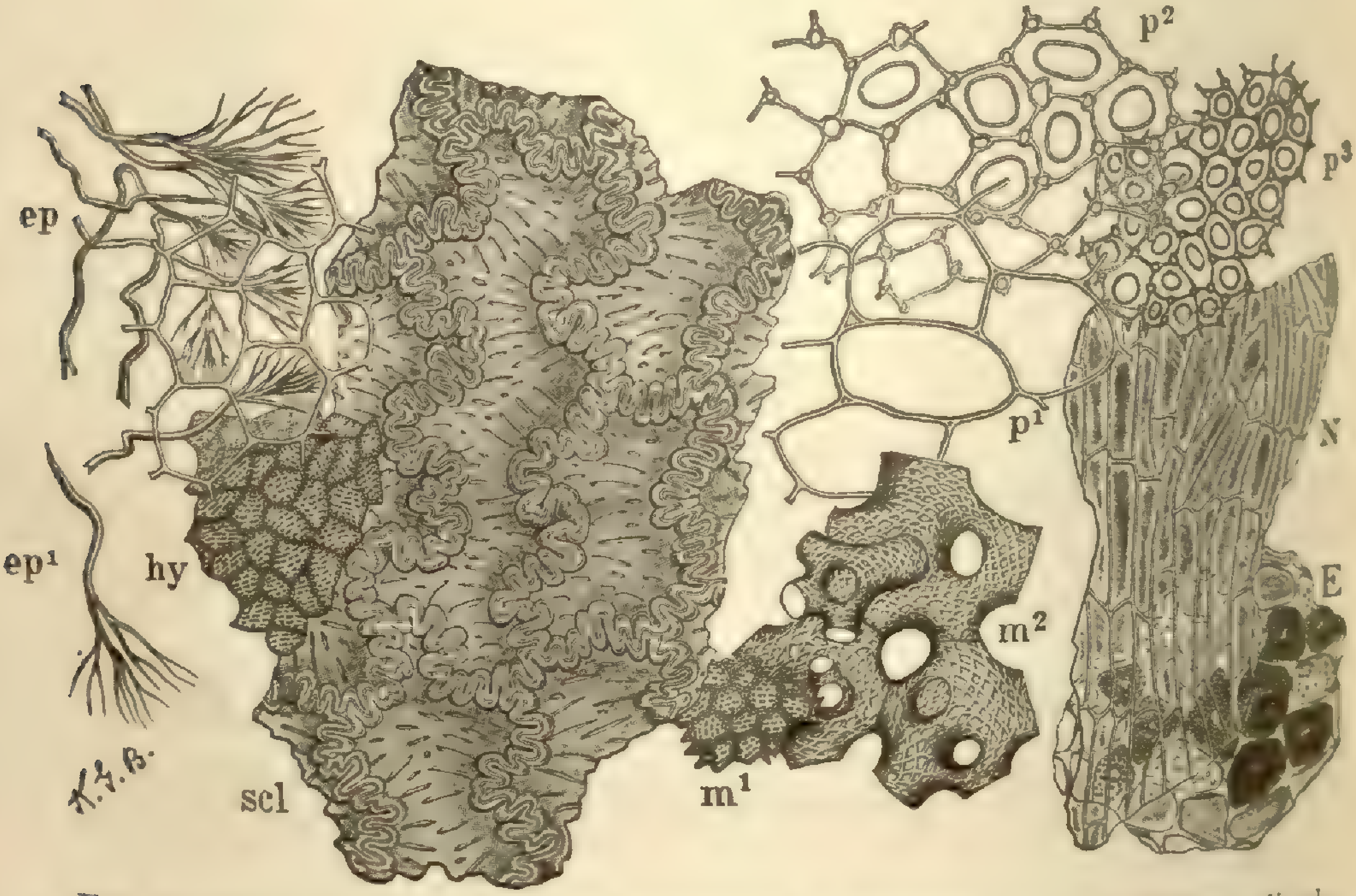


FIG. 5.—*Cucurbita Pepo* L. Seed elements in surface view; *ep*, ribbed palisade cells of epidermis; ep^{1}, isolated rib; *hy*, subepidermal layer; *scl*, sclerenchyma; m^{1}, pitted parenchyma; m^{2}, reticulated spongy parenchyma; p^{1}, parenchyma; p^{2}, spongy parenchyma; p^{3}, inner epidermis of spermoderm; *N*, perisperm; *E*, endosperm. ×160.

Round starch grains (*am*), up to 7 μ in diameter, of the type already described, occur in considerable numbers in the epidermal cells.

2. *Subepidermal layer* (*hy*).—Below the epidermis is a layer of

small, polygonal, somewhat elongated cells, about 25 μ in diameter, with numerous minute pits, giving the walls a beaded appearance. This layer, without intercellular spaces, is three to five cells thick, the number increasing toward the edge of the seed.

3. *Sclerenchyma* (*scl*).—Firmness is given to the spermoderm by one layer (over the edge two or three) of longitudinally elongated (250 μ) cells, arranged end to end in rows. In surface view, both side and end walls are sinuous, often reaching 20 μ in thickness. After maceration and by careful focusing, the outer and inner surfaces of these cells may be seen to send out remarkable ramifications, whose dichotomous branches overlap one another. In transverse section the oval appearance of the cell cavity is a characteristic feature. A few pits may be seen with a high power.

4. *Parenchyma.*—There are three quite distinct layers, the parenchyma showing the greatest differentiation in this species. In contact with the sclerenchyma is the first layer of small pitted cells, with few or no intercellular spaces (m^1). Resting on this compact layer, either singly or in groups, are larger cells, which stand out like branches in the intercellular spaces of the next layer.

The cells of the second layer are characteristic of the genus (m^2). In this species the layer is two cells thick, with intercellular spaces so large that they form a great cavity in which the cells are suspended. In form the cells are somewhat stellate, joining the preceding layer by one branch or a similar but smaller cell. The walls are beautifully reticulate, the thickenings following a definite course around the curved surface of the cell. The cross walls are netted in a similar manner but with a somewhat larger mesh.

The true spongy parenchyma consists of a number of layers of somewhat collapsed cells, but treatment with Javelle water expands the tissues so that they may be easily studied. The cells are thin-walled, decreasing in size toward the inner epidermis (p^1, p^2). In surface view the contour of the branches appears, in the center of the cells, as rings nearly as large as the cells themselves. A green color is given to these inner layers by chlorophyll.

5. The *inner epidermis* (p^3) is composed of small, thin-walled cells.

PERISPERM (*figs. 5, 6, N*).—In this coat there are about six layers of thin-walled cells with longitudinally elongated, cuticularized epidermal cells.

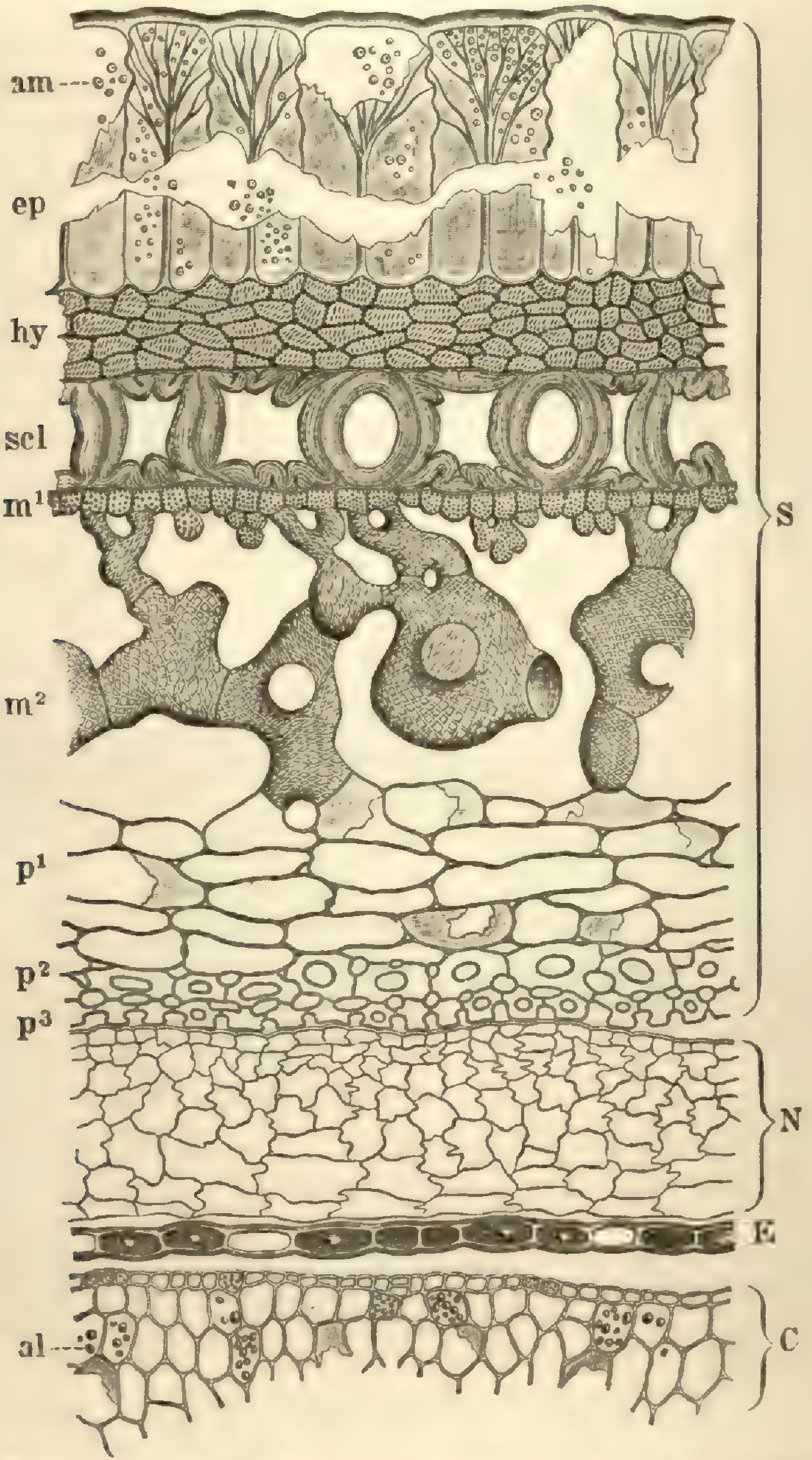


FIG. 6.—*Cucurbita Pepo* L. Seed in cross-section; *S*, spermoderm consisting of *ep*, ribbed palisade cells of epidermis containing *am*, starch grains, *hy*, pitted subepidermal layer, *scl*, sclerenchyma, m^1, pitted parenchyma, m^2, reticulated spongy parenchyma, p^1, parenchyma, p^2, spongy parenchyma, and p^3, inner epidermis; *N*, perisperm; *E*, endosperm consisting of aleurone cells; *C*, cotyledon containing *al*, aleurone grains. ×160.

ENDOSPERM (*figs. 5, 6, E*).—This consists of a single layer of cells with thickened walls, containing granular protoplasm and a large central nucleus.

EMBRYO.—The cotyledons (*C*) have small epidermal cells on both surfaces and two layers of palisade cells within the inner epidermis. Aleurone grains (*al*) up to 6 μ, containing globoids and crystalloids, also oil, are found in all the cells.

C. PEPO VAR. VERRUCOSA NAUD.

This variety, the crook-necked squash, has a rather large flask-shaped fruit, with the neck showing a distinct curve or crook. Longitudinal grooves occur frequently, but are not so well marked as in *C. Pepo.* There is a hard rind, yellow or orange in color, covered with very pronounced warts and filled with bundle fibers. The central parenchymatous tissue breaks down only in the swollen base, the neck not expanding enough to tear the tissues apart.

The seeds, of a dirty white color, are not over 2^{cm} long, smooth, and flattened, with a border at the edge.

PERICARP (*fig. 7*).—The pericarp of this variety differs very little from that of *C. Pepo,* the chief difference being in the greater hardness of the rind.

1. *Epicarp* (*epi*).—The palisade layer is about 36 μ in height, the thickened, prismatic cells having cuticularized outer and radial walls. The outer wall is not uniformly thickened; instead it has a depression over each cell, giving it a wavy contour in cross-section.

There are two forms of hairs, resembling those of *C. Pepo* in size and shape; instead of falling off, however, they persist on the mature fruit. Sunken stomata (*sto*) are present in considerable numbers.

2. *Hypoderm* (*hy*).—The cells of this layer resemble those of *C. Pepo*, the description given for that species applying to this.

3. *Outer mesocarp* (*st*).—This characteristic layer consists of many layers of stone cells which differ considerably in size. The cells are polygonal, small in the sharply defined outer layer, increasing in size inward until they are lost in the next cell layer. About spherical cavities (*x*), occurring at the junction of this layer with the hypoderm, the cells elongate radially to about twice their transverse diameter. These cavities are really large intercellular spaces appearing in the young fruit and showing no evidence of secreting cells in any stage of growth. Before the walls thicken the cells bulge out into these cavities. Among the smaller polygonal cells are also large spherical

ones with cell cavity, frequently 150 μ in diameter, about the size of the intercellular cavities, both being conspicuous. The cell walls vary from 8–14 μ in thickness and have numerous pits.

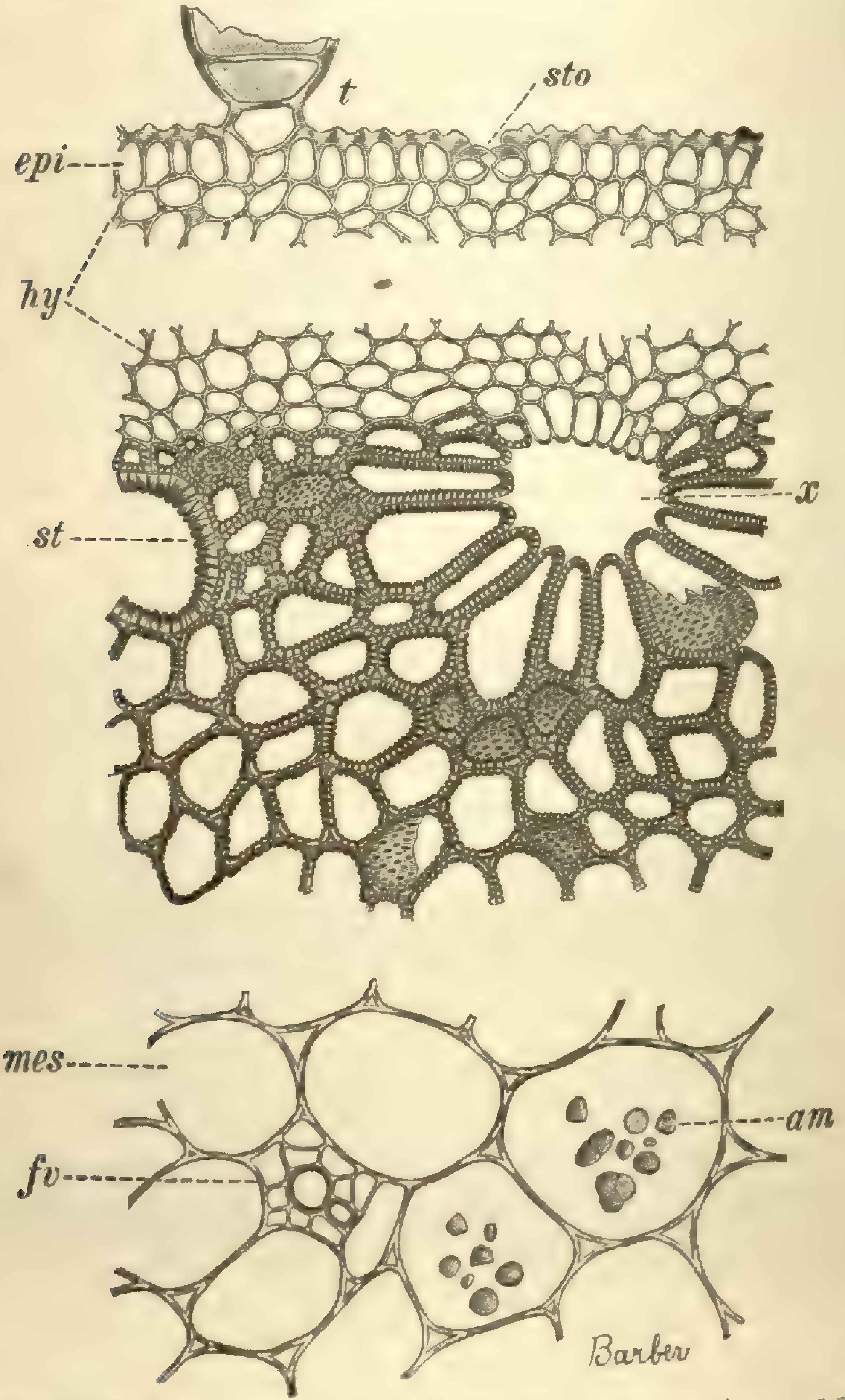


FIG. 7.—*Cucurbita Pepo* var. *verrucosa* Naud. Pericarp in cross-section; *epi*, epicarp with *t*, hair, and *sto*, stoma; *hy*, hypoderm; *st*, outer mesocarp (stone-cell layer) with *x*, spherical cavity; *mes*, middle mesocarp with *fv*, bundle, and *am*, starch. ×160.

4. *Middle mesocarp* (*mes*).—The middle layers of the mesocarp consist of rather thick-walled cells containing numerous truncated starch grains (*am*).

5. *Inner mesocarp.*—The cells of the inner layers are the same size as those of the middle mesocarp, but have thinner walls, larger intercellular spaces, and no evident contents. The fibrovascular bundles, sieve tubes, and latex tubes, found throughout the tissues, are of the usual type.

6. *Endocarp.*—This layer corresponds with that of the species already described.

SPERMODERM.—This differs from that of *C. Pepo* only in the first and fourth layers, as follows:

1. *Epidermis.*—The thickenings on the radial walls, besides branching profusely at the outer end, send out occasional fine branches the whole length of the rod.

4. *Parenchyma.*—The second layer of this parenchyma is four or five cells thick, with somewhat smaller intercellular spaces than in *C. Pepo.*

C. PEPO VAR. MELOPEPO L.

The popular name (scallop) for this variety suggests the shape of the fruit. It is a large depressed berry with ten to fifteen quite deeply cut longitudinal grooves. Like *C. Pepo* it is firm, smooth, and yellow, with a rind and a central cavity containing fibers.

The seeds are elliptical, 1–1.5^{cm} in length, smooth, flattened, bordered, and of a yellow-white color.

PERICARP.—The cell structure does not differ essentially from that of *C. Pepo.*

SPERMODERM.—This coat differs slightly from the corresponding coat of *C. Pepo.* The palisade layer, with thickenings like those of the variety *verrucosa*, is thicker, reaching 0.3^{mm} on the flattened surface of the seed.

The *raphe*, which in the species previously described is found only around the edge of the seed, here sends out a few branches over the sides. In cross-section the cut surfaces of these branches are quite evident in the inner parenchyma.

C. PEPO VAR. OVIFERA NDN.

The fruit of this variety is egg-shaped, 8–10^{cm} long, of a yellow-white color, with hard rind which dries up and persists in its original form. The rind is 1^{cm} thick surrounding the central mass of fibers, which do not break down. A cavity is formed, but it is not so evident as in the other species of this genus, since the tissues, although separating, retain their original position.

The seeds are of the usual type for this genus.

PERICARP.—The layers are essentially like those of the variety *verrucosa*, having a wavy-walled *epicarp*, thick-walled *hypoderm*, *outer mesocarp* of stone cells with the characteristic cavities and large spherical cells, *middle mesocarp* with starch, etc.

SPERMODERM.—The layers are similar to those already described.

C. PEPO VAR. ORANGINA SER.

The fruit of this variety differs from that of the type only in macroscopic appearance, having the size, shape, and color of the orange. Rigidity is given the thin rind by the *outer mesocarp* of stone cells.

The small seeds are histologically like those of the preceding variety.

CUCURBITA MAXIMA DUCH.

This species (winter squash) is a native of southern Asia and, like *C. Pepo*, has many varieties differing in size and shape.

The fruit, the largest of the family, varies from 15 to 90^{cm} in length. It is rounded ovate, with warts and occasional longitudinal grooves, and is of a yellow, orange, or green color. In the so-called "turban" variety, the top of the fruit projects beyond an encircling line, or constriction, which marks the margin of the adherent receptacle. The hollow rind with central cavity is filled with bundles and seeds.

The white seeds are 1.5–2.5^{cm} long, smooth, and flattened, with a border.

Both fruit and seed closely resemble in structure *C. Pepo* and its varieties.

PERICARP.—The thin *epicarp*, small-celled *hypoderm*, sclerenchymatized *outer*, thin-walled *middle*, and *inner mesocarp* are like those of *C. Pepo* var. *verrucosa* (*fig. 7*).

SPERMODERM.—The chief difference between this coat and that of the species already described is in the middle spongy parenchyma, which in this seed is five to six cells thick.

Cucumis sativus L.

Cucumis sativus L. (cucumber) occurs native in the East Indies, and from this species have been derived many varieties which have long been cultivated in gardens.

The fruit varies in size, but is always elongated or oval, and rounded triangular in cross-section. It is fleshy and solid, without a central cavity, and of a yellow-white color with white fruit-flesh. Numerous warts cover the surface, each capped with a short blunt spine which readily becomes detached during growth or on handling.

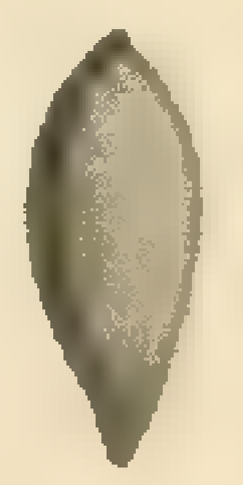
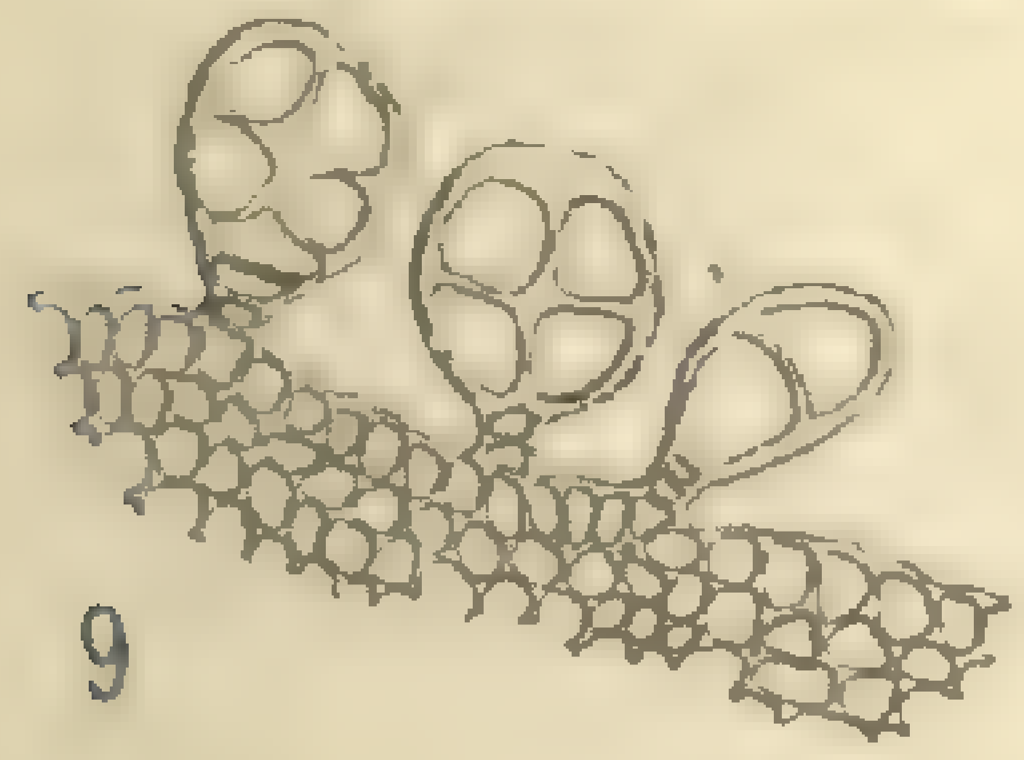


Fig. 8.—*Cucumis sativus* L. Seed. ×1.

Numerous white seeds (*fig. 8*), borne within the three locules, are 1–1.5^{cm} in length, flattened, seldom over 2^{mm} thick, and are not, like those of Cucurbita, provided with a border.

Pericarp (*figs. 9, 11*).—This consists only of the solid fruit-flesh, the bundles occurring throughout the mesocarp and not in a central cavity.

1. *Epicarp* (*epi*).—The prismatic cells form a palisade layer 75 µ in width, with strongly thickened outer and radial walls, and very thin inner ones. The intense color of the fruit is due, not to the cell contents, but to the yellow walls.



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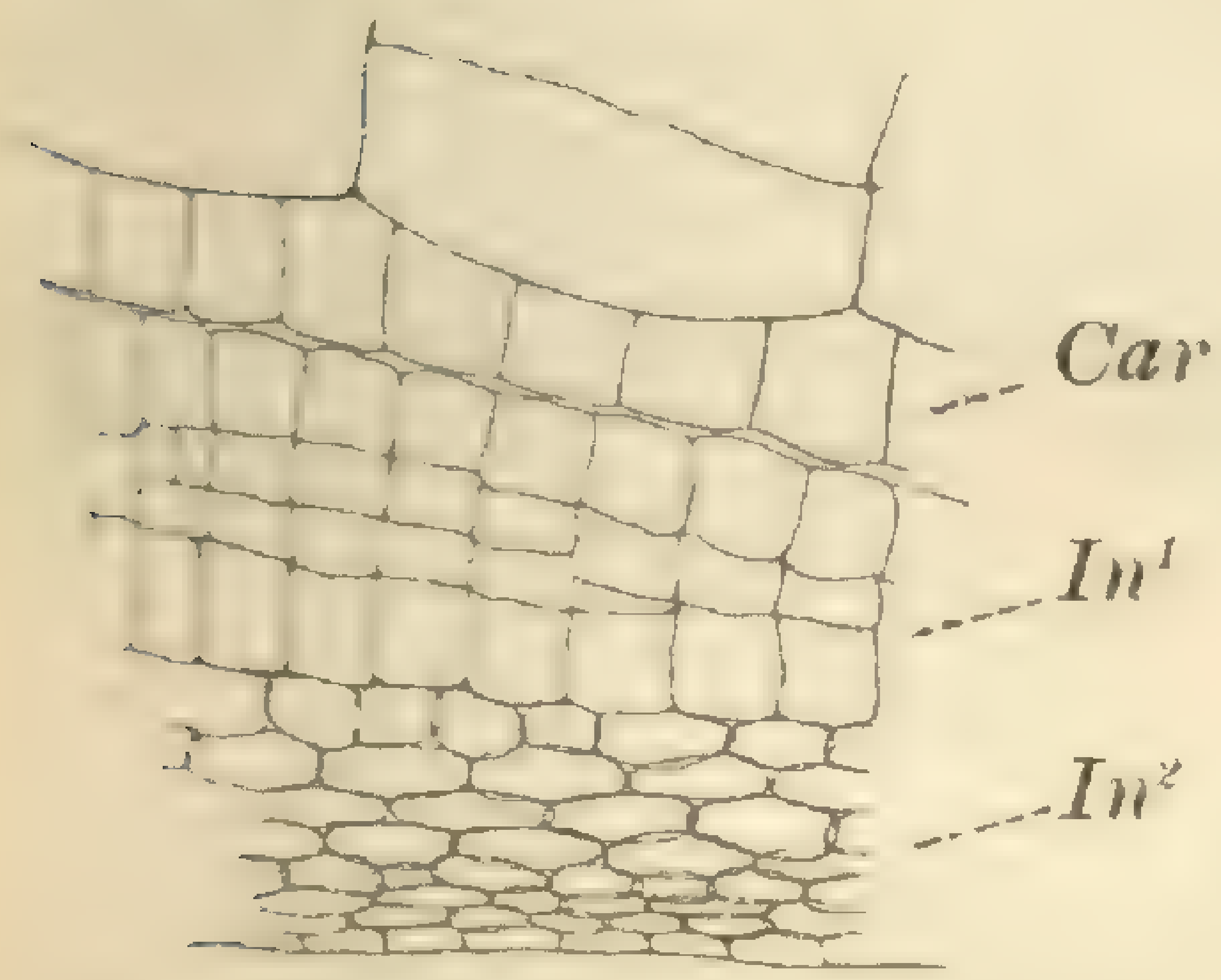

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Fig. 9. *Cucumis sativus* L. Immature epicarp in cross-section, with glandular hairs. ×160.—Fig. 10. *Cucumis sativus* L. Immature seed in cross-section: *Car*, inner carpellary layer; *In*¹, outer integument; *In*², inner integument. ×200.

The warts, which appear before fertilization of the flower, have the same cell structure as the outer layers of the pericarp. Each bears an emergence (*fig. 11*) consisting of large cells with thickened, sparingly pitted walls. They grow rapidly for a short time, but lose their contents soon after their walls begin to thicken.

At its apex the emergence bears a long, jointed (up to ten cells), conical hair, with thickened walls. The cross walls and inner sunken foot, also thickened, are pitted (*t*).

Occasionally a second hair, similar in structure but of smaller size, is developed at the side of the terminal one. The hairs usually disappear in the early stages of growth, but the emergence, unless rubbed off, persists as a brown hyaline spine.

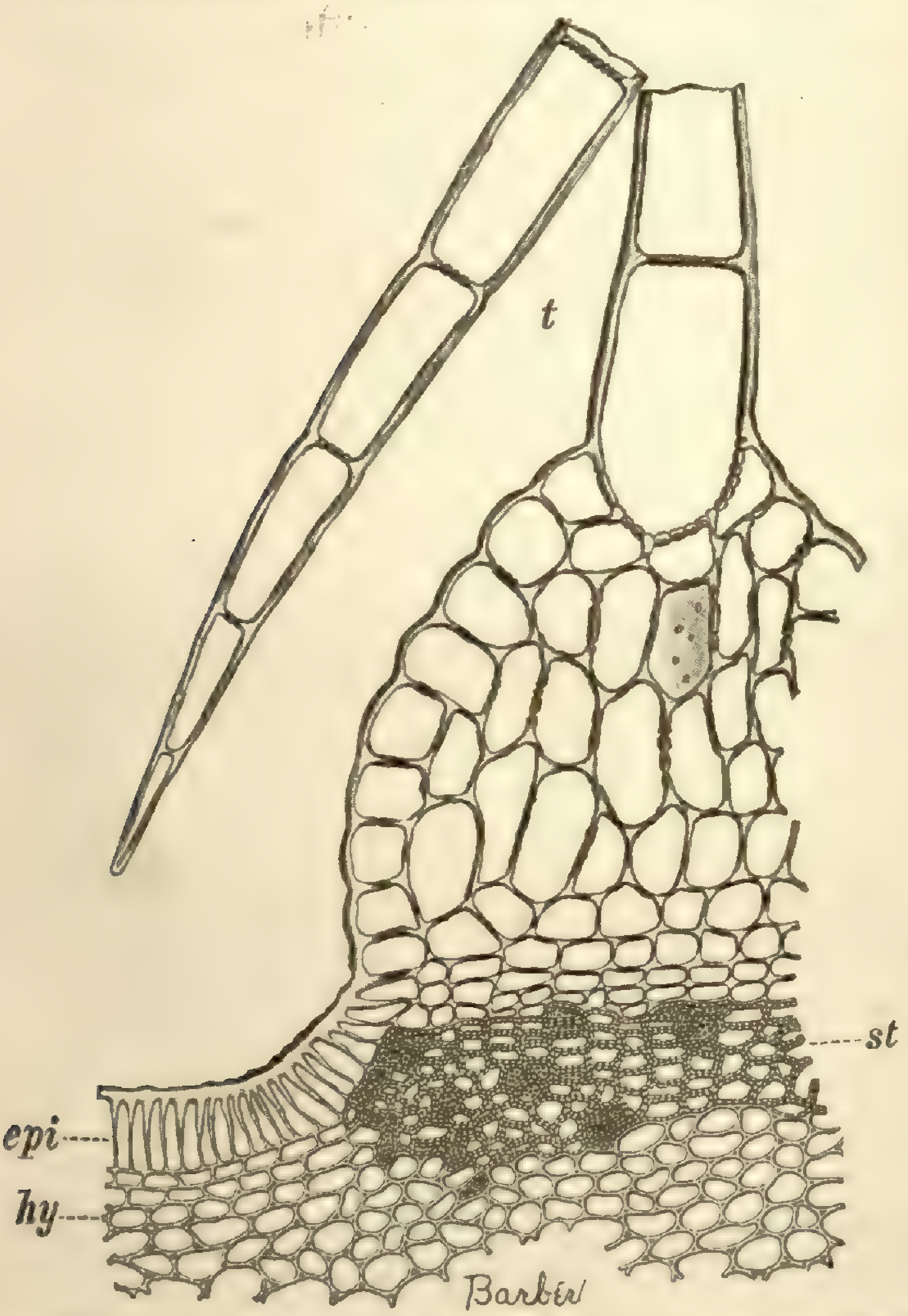

FIG. 11.—*Cucumis sativus* L. Pericarp in cross-section; *epi*, epicarp with emergence bearing *t*, hair; *hy*, hypoderm; *st*, sclerenchymatized cells at base of hair. ×55.

In addition to the hairs of the wart, numerous small capitate hairs, consisting of a four-celled head and stalk of three cells, cover the immature fruit, but disappear early, leaving no scars. Stomata are not present.

2. *Hypoderm* (*hy*).—A number of layers of small, rounded, loosely arranged cells form the subepidermal tissues. In the young fruit they are filled with chlorophyll grains which entirely disappear at maturity.

At the base of the emergence occurs a group of hypodermal cells which become thickened, sclerenchymatized, and pitted (*st*). This thickening of the cell walls probably serves either to prevent evaporation, or entrance of fungi, or both, after the removal of the emergence. In leguminous seeds there are sclerenchyma cells immediately below the hilum groove which serve this same purpose.

3. *Outer mesocarp*.—MOELLER[22] finds a weakly developed stone

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[22] Mikroskopie der Nahrungs- und Genussmittel 473.

cell layer. In the many fruits I have examined, however, the mesocarp does not show any great differentiation. The outer layers consist of rather small thin-walled cells with intercellular spaces.

4. The *middle mesocarp* differs from the outer only in the greater size of the cells.

5. In the *inner mesocarp* the cells become smaller, resembling those in the outer mesocarp. The bundles, isolated sieve tubes, and latex tubes, found throughout the mesocarp, are of the type already described.

6. *Endocarp.*—The elongated, thin-walled cells of this layer remain with the mesocarp and are not attached to the seeds as in Cucurbita.

SPERMODERM (*figs. 10, 12–14*).—Seeds for study should be taken directly from the fruit, as in drying they usually lose their outer walls.

1. *Epidermis* (*fig. 12, ep*).—The prismatic cells are radially elongated to 160 μ on the sides of the seed and 260 μ at the edge. In surface view they are polygonal, transversely elongated, and arranged side by side in rows. The outer and inner walls are thickened, the outer having in addition a cuticle, while the radial walls are very thin, with the characteristic thickenings on only the side walls. Each thickening consists of a single straight rod, broadened at the base and tapering rather abruptly into a blunt almost rounded point just within the cuticle. VON HÖHNEL,[23] in the year 1876, described these rods as consisting of two different layers; FICKEL,[24] the same year, found three; and HARZ,[25] although quoting VON HÖHNEL, pictured three. My own observations corroborate FICKEL's statement. The three layers can be distinguished by the difference in refractive power and by staining. The inner layer, which gives the color reaction for lignin, shows the strongest refraction; this is surrounded by a thin layer of cellulose (blue with iodin and sulfuric acid) of rather weak refractive power; and this in turn is inclosed in a broader, scarcely visible, second layer of cellulose (also taking the blue stain). Tangential sections show the arrangement of the layers and the elliptical appearance of the cut rods.

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[23] *Loc. cit.*, footnote 3, p. 330.

[24] *Loc. cit.*, footnote 2, p. 742.

[25] *Loc. cit.*, footnote 7, p. 773.

2. *Subepidermal layer* (*sub* and *fig. 13*).—On the flattened surface of the seed this tissue consists of one layer of longitudinally elongated cells, arranged end to end in rows, while at the edge they are somewhat shorter and form several layers. They are quite large, ranging from 50–175 μ in length, and have thickened and sclerenchymatized sinuous walls. The most striking feature of the layer, best seen in surface view, is the intercellular spaces which occur in great numbers between the side and end walls. They are very small, several occurring in every turn of the sinuous wall, which is greatly thickened about the space. Between these spaces and also in the outer and inner walls are small pits.

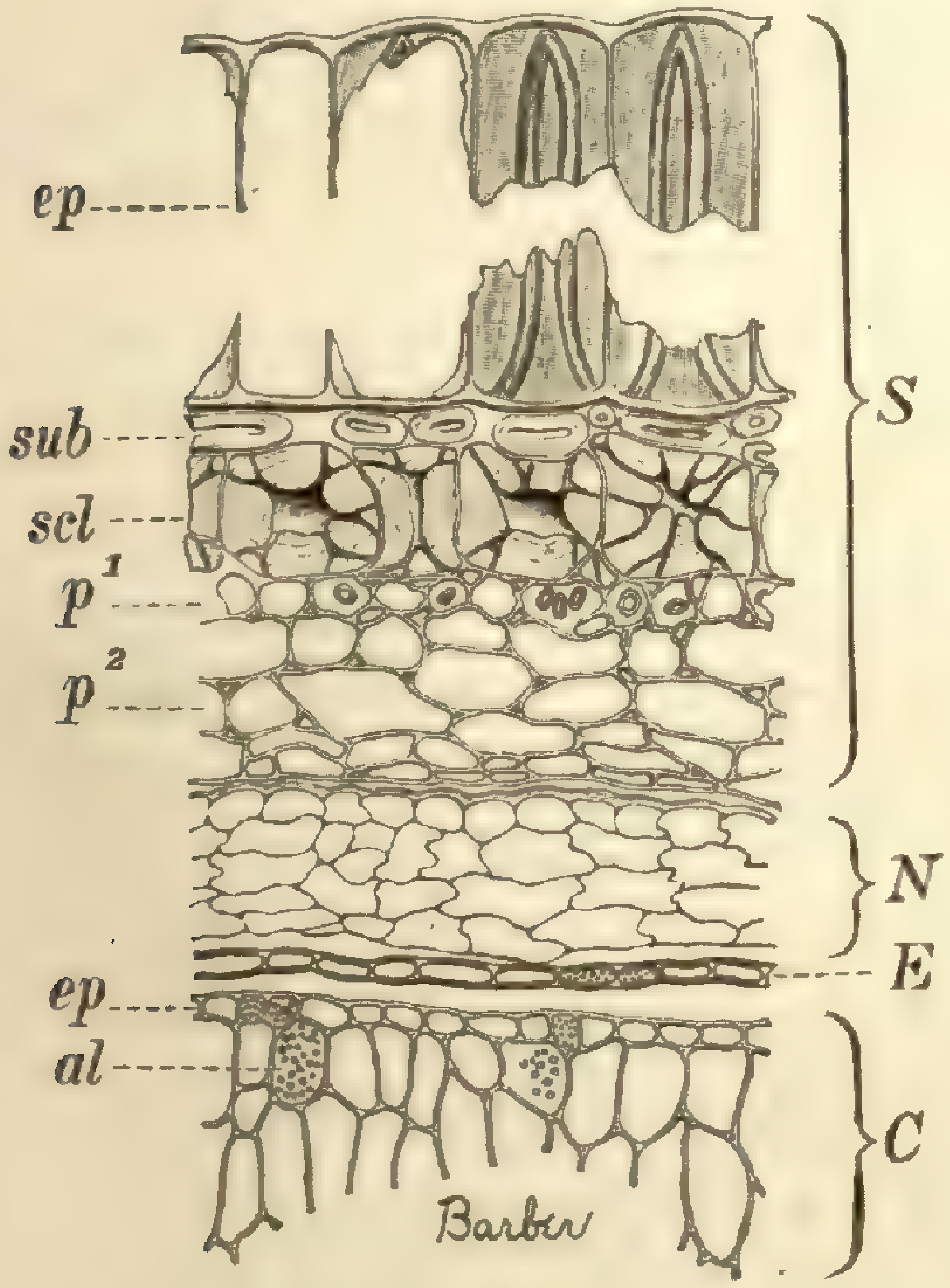

FIG. 12.—*Cucumis sativus* L. Seed in cross-section. *S*, spermoderm consisting of *ep*, epidermis, *sub*, subepidermal layer, *scl*, sclerenchyma, p^1, stellate parenchyma, p^2, spongy parenchyma; *N*, perisperm; *E*, endosperm; *C*, cotyledon consists of *ep*, epidermis and mesophyll with *al*, aleurone grains. ×160.

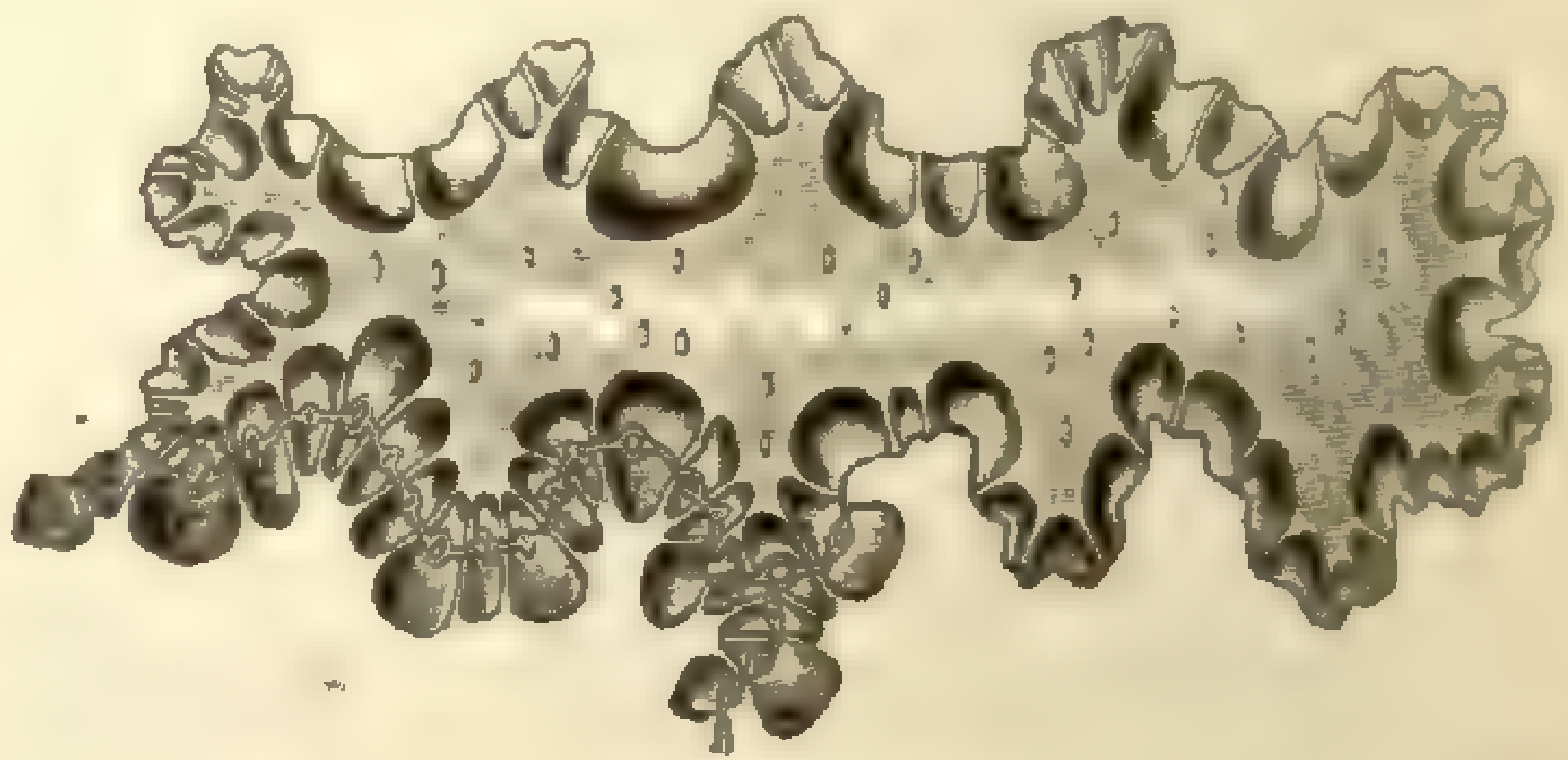

FIG. 13.—*Cucumis sativus* L. Isolated subepidermal cell of spermoderm in surface view. ×300.

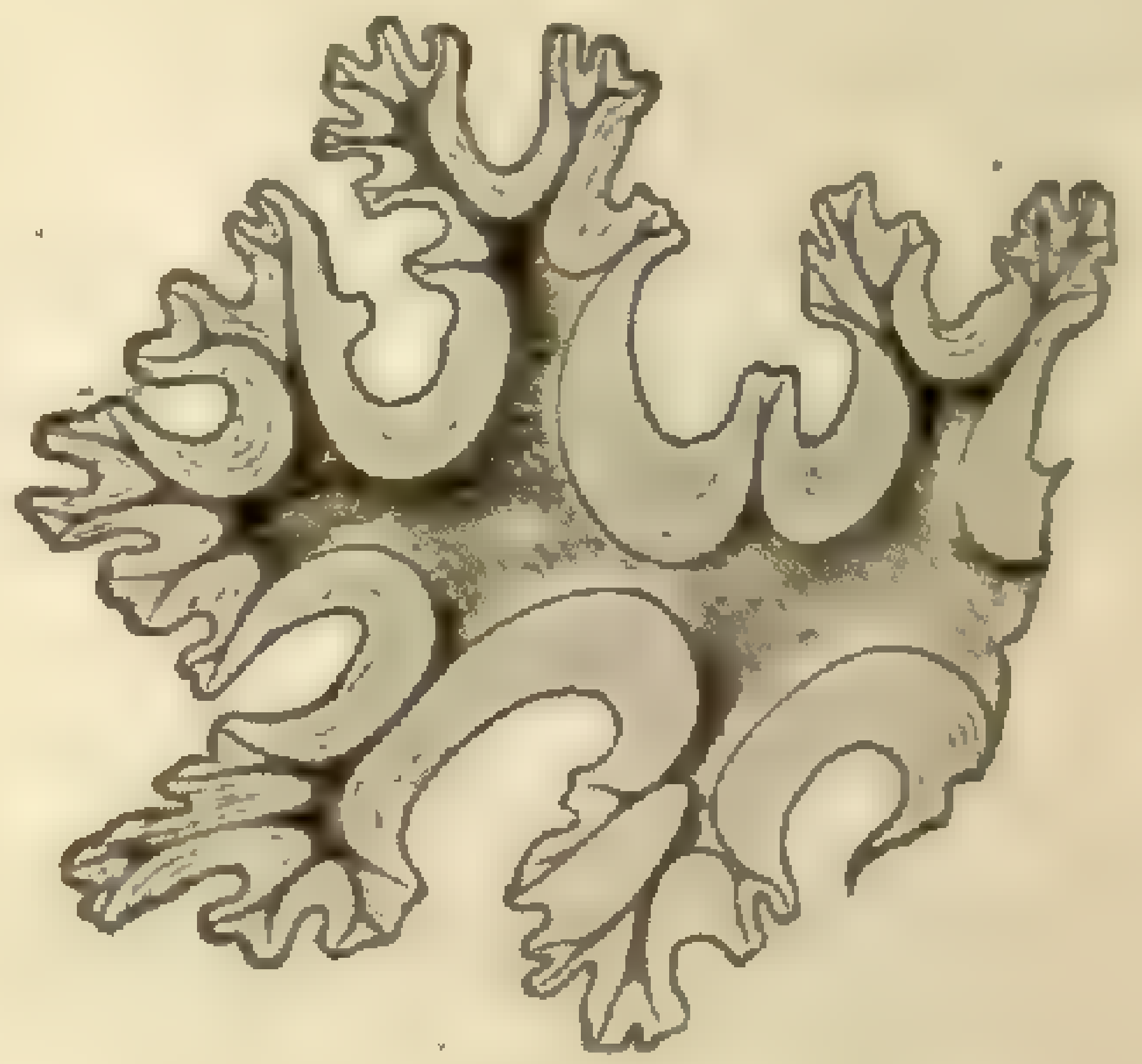

FIG. 14.—*Cucumis sativus* L. One-half of isolated cell of sclerenchyma layer in surface view. ×300.

3. The *sclerenchyma* (*scl* and *fig. 14*) consists of one layer (more toward the edge) of longitudinally elongated (220 μ) cells with narrow cell cavities and very thick lignified walls. Heating with potash brings to view the middle lamella and striations of the wall, but

only after maceration can the overlapping branches of the ramifications be seen. Pits are numerous.

4. *Parenchyma.*—The outer layer (p^1) is one cell thick at the side, increasing in number toward the edge, and consists of small cells more or less stellate in form. This layer is followed by two or three cell layers of thin-walled parenchyma (p^2), which are usually ruptured in dry seeds.

5. The *inner epidermis* consists of small, elongated parenchyma cells.

PERISPERM (*N*).—A number of layers of collapsed, thin-walled cells form this layer. The longitudinally elongated epidermal cells have a cuticle.

ENDOSPERM (*E*).—The cells of this layer are polygonal, 22 μ in diameter, have thickened walls, and contain small proteid granules.

The EMBRYO (*C*) lacks distinctive features.

CUCUMIS MELO L.

All the varieties of musk melon are derived from a single species indigenous to Africa and Asia. HARZ divides the species into nine groups, each with one to ten subspecies.

The fruit varies somewhat in size and shape, but is usually spherical, oval, or occasionally elongated, and has eight to ten longitudinal grooves, differing in depth in different specimens, to which is due the characteristic "melon shape." The surface is green, yellow, or red, with a gray network of corklike tissue.

A rind 2.5 to 5^{cm} thick, with yellow to reddish fruit-flesh, incloses a central cavity containing fibers, seeds, and a considerable amount of watery fluid.

The seeds are like those of *C. sativus*, except that their color is yellow.

PERICARP (*figs. 15–17*).—This consists of the hard rind, and the soft, sweet watery fruit-flesh with bundles.

1. *Epicarp* (*epi*).—The cells of this layer vary in size, shape, and thickness of walls. On the ribs there is a palisade layer of greatly thickened, polygonal cells with a cuticle. In the grooves the cells increase in size, the walls become thinner, and pits make their appearance. In cross-section the cell cavity appears flask-shaped, the

neck running out to a point. *Fig. 15* shows the radiating cell cavity in tangential section.

According to MOELLER,[22] cork cells occur here and there below the epicarp. This I find to be true of the young fruit, but at maturity they break through the epicarp, forming the corky ridges or netted thickenings previously mentioned. The cells are small, thin-walled, and radially arranged, forming a dense mass of cork tissue, which, together with the ruptured epicarp, closely resembles lenticels, but no complementary cells are formed. This likeness is very marked in cross-section (*fig. 16*).

Stomata (*fig. 17, sto*), with guard cells of the usual type, are present in the grooves and, less frequently, in the depressions between the corky ridges. The walls of the accompanying cells have few or no pits and are irregularly thickened. In some instances the whole wall is thickened, while in others large protuberances are sent out into the cavity.

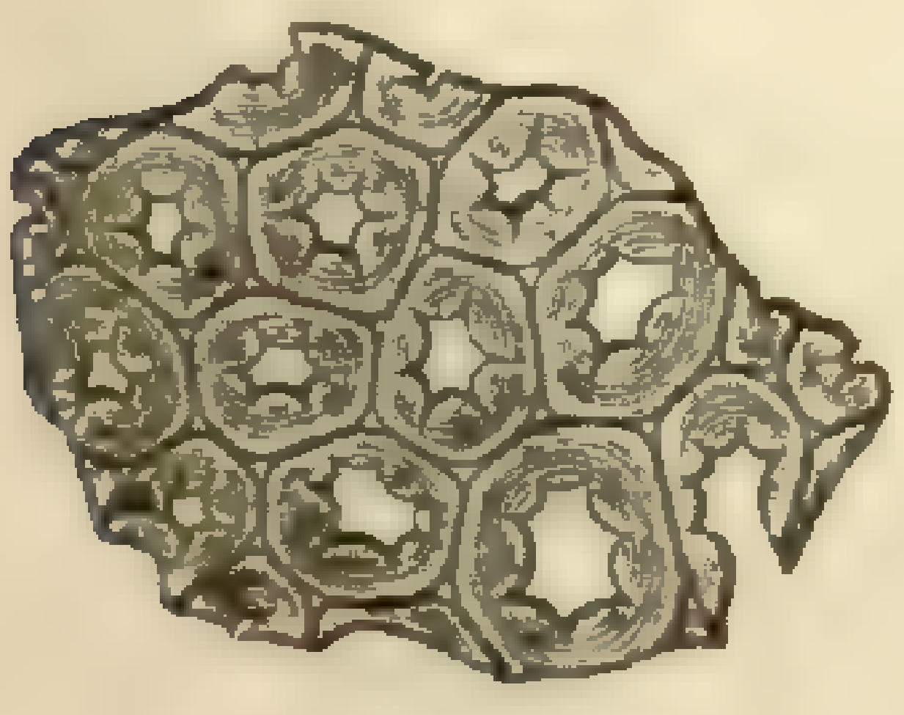

FIG. 15.—*Cucumis Melo* L. Epicarp in tangential section. ×160.

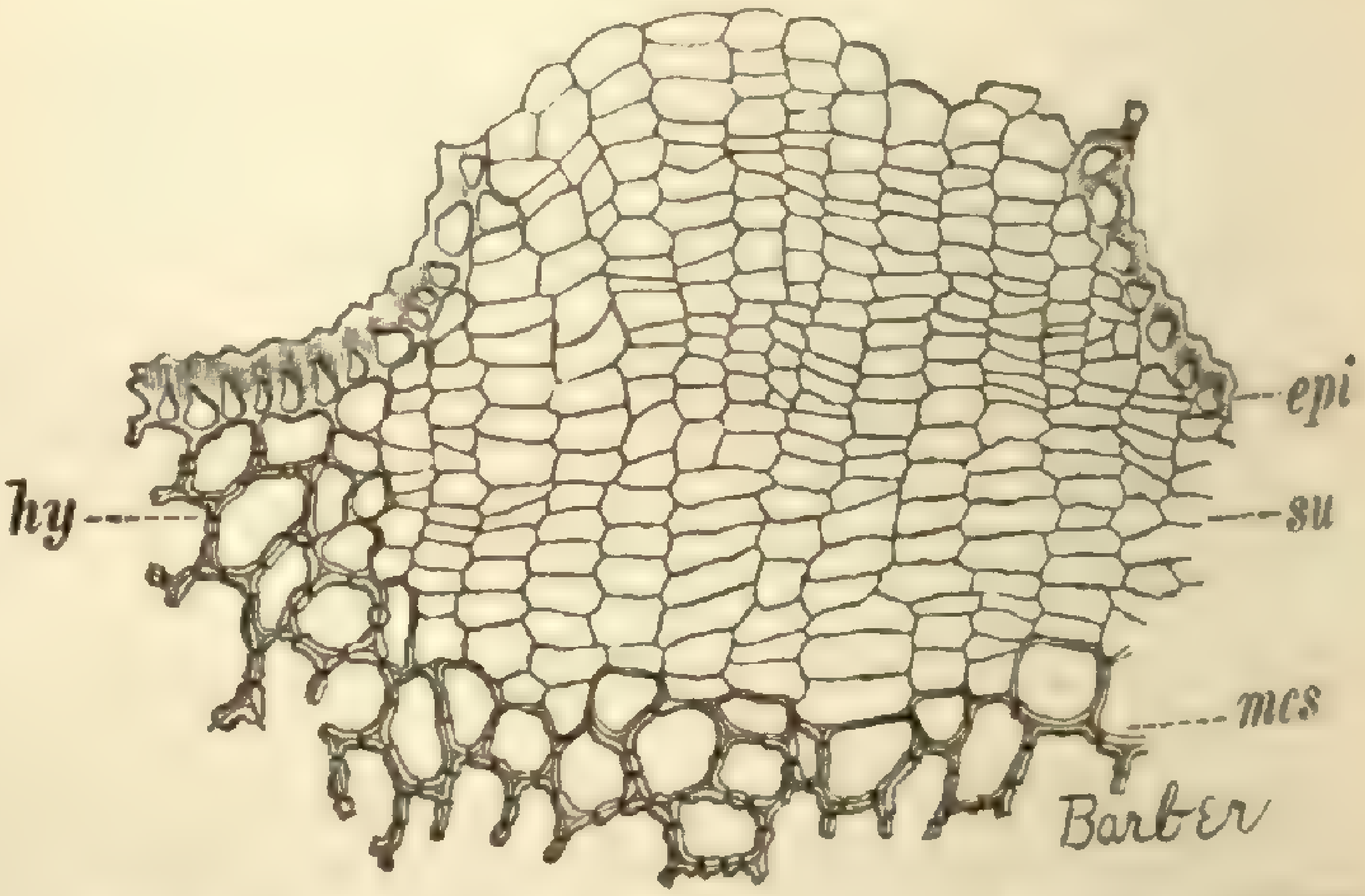

FIG. 16.—*Cucumis Melo* L. Rib of pericarp in cross-section; *epi*, epicarp; *su*, cork; *hy*, hypoderm; and *mes*, mesocarp. ×50.

In the depressions and grooves are jointed (three or more cells), conical hairs up to 375 μ in length (*t*). The diameter at the base is the same as that of the neighboring cells, but gradually diminishes to the apex. The thickened walls have additional minute local thickenings or warts, visible only by the most careful focusing. About the hair scars the cells are distinguished by the smaller cavities and thicker walls.

The immature fruit bears small capitate hairs like those of *C. sativus.*

2. *Hypoderm* (*hy*).—The cells of a number of layers beneath the epicarp are thickened and pitted. Below the thick-walled epidermal cells they are of medium size with intercellular spaces; under the thinner epidermis of the grooves, through which they are visible, they are larger and thinner-walled with very large pits. Chlorophyll is present in greater or less amount even though the fruit appears yellow.

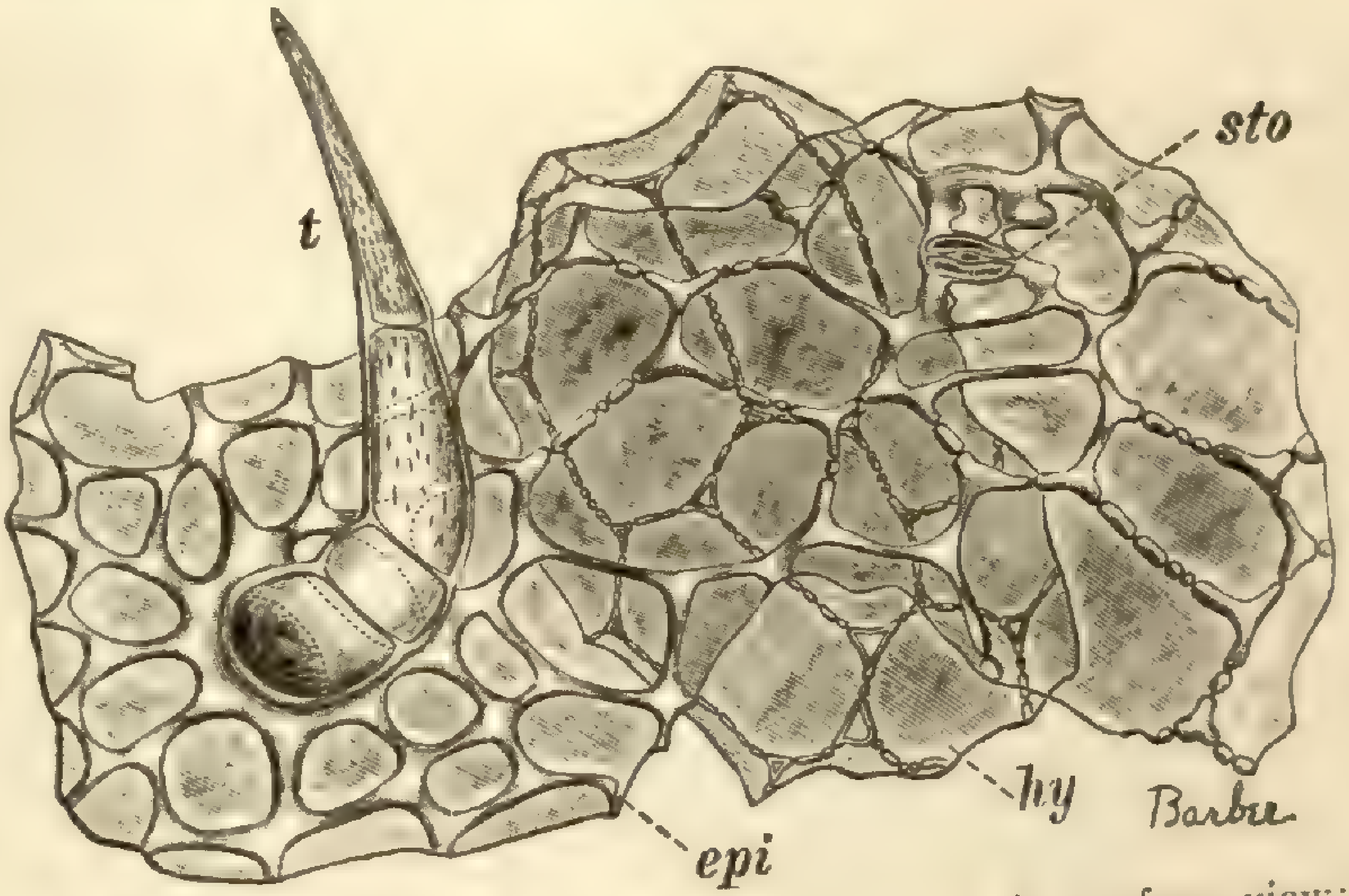

FIG. 17.—*Cucumis Melo* L. Pericarp in surface view; *epi*, epicarp with *t*, hair, *sto*, stoma; *hy*, hypoderm. ×160.

3, 4, 5. The *outer*, *middle*, and *inner mesocarp* of this species consist of cells similar to those of the corresponding layers of *C. sativus*. The placentae, however, instead of persisting intact, are almost if not quite broken down.

6. *Endocarp*.—As in *C. sativus*, the cells are thin-walled and longitudinally elongated.

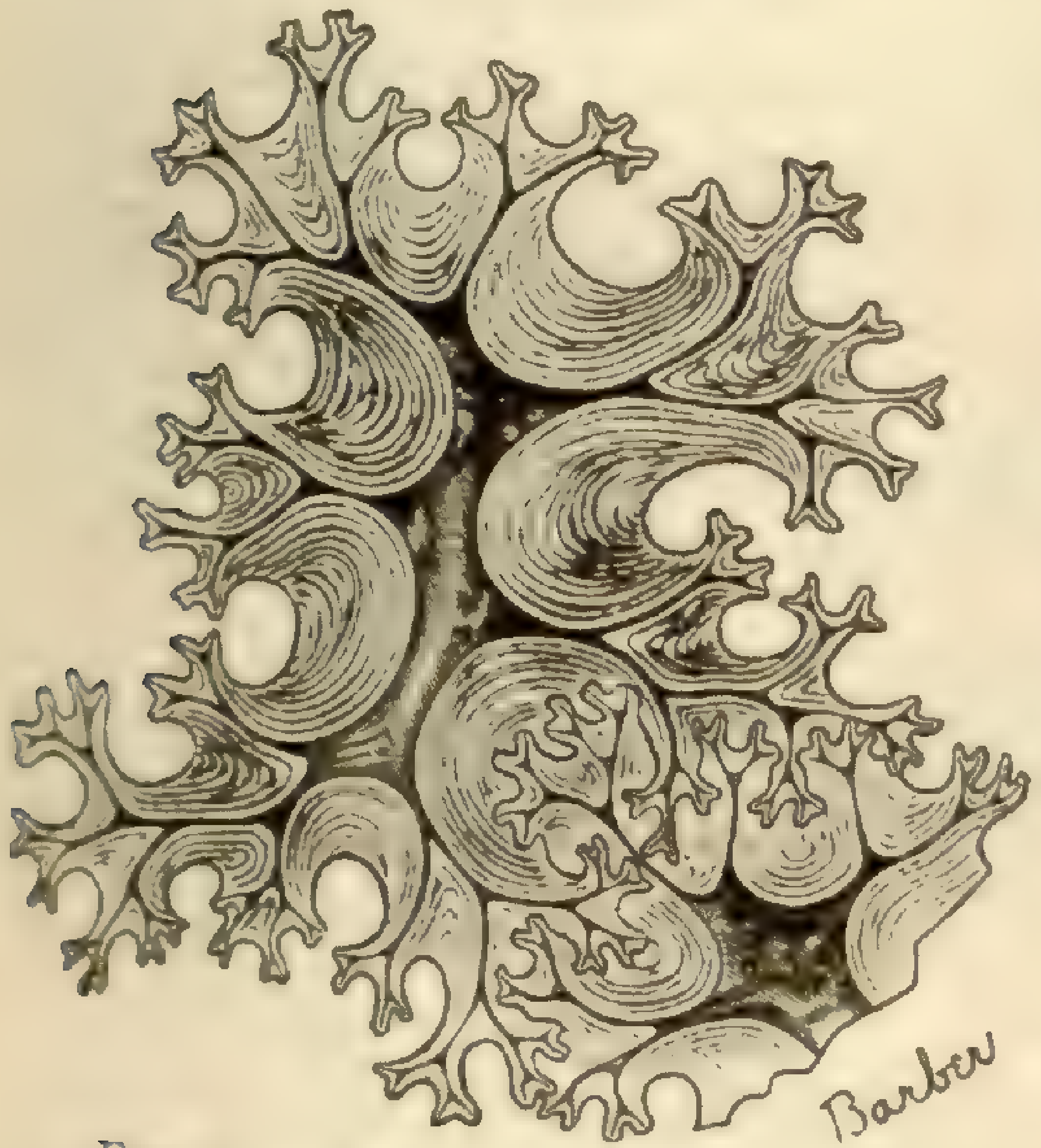

FIG. 18.—*Cucumis Melo* L. Seed in cross-section; *S*, spermoderm consisting of *ep*, epidermis, *sub*, subepidermal layer, *scl*, sclerenchyma, p^1, sclerenchymatized spongy parenchyma, p^2, spongy parenchyma; *N*, perisperm; *E*, endosperm; *C*, cotyledon with *ep*, epidermis, and mesophyll containing *al*, aleurone grains. ×160.

SPERMODERM (*fig. 18*).—1. *Epidermis* (*ep*). Seen in surface view the cells are polygonal and in cross-section they reach a length of 200 μ. The outer wall is thickened and the thin radial walls have the characteristic thickenings. HARZ[26] figures this layer with rods having small side branches at right angles, and MOELLER[22] describes them as simple rods without branches. Like the latter author, I find single straight rods, one on each radial wall, which stain yellow with iodin and sulfuric acid, thus showing them to contain lignin.

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[26] *Loc. cit.*, footnote 7, p. 777.

2. The *subepidermal layer* (*sub*) is the most characteristic layer of this seed. Whereas in *C. sativus* it consists of but one cell layer, in this species it has five or six layers of cells longitudinally elongated (except at the edges) and arranged end to end in rows. Both species have sinuous walls and characteristic circular intercellular spaces visible in cross- as well as in longitudinal section. The cells of the outer layer are small, increasing inward in size and thickness of wall with every layer, until the inner one is distinguished from the sclerenchyma only by the somewhat more irregular arrangement and the slightly smaller size of the cells.

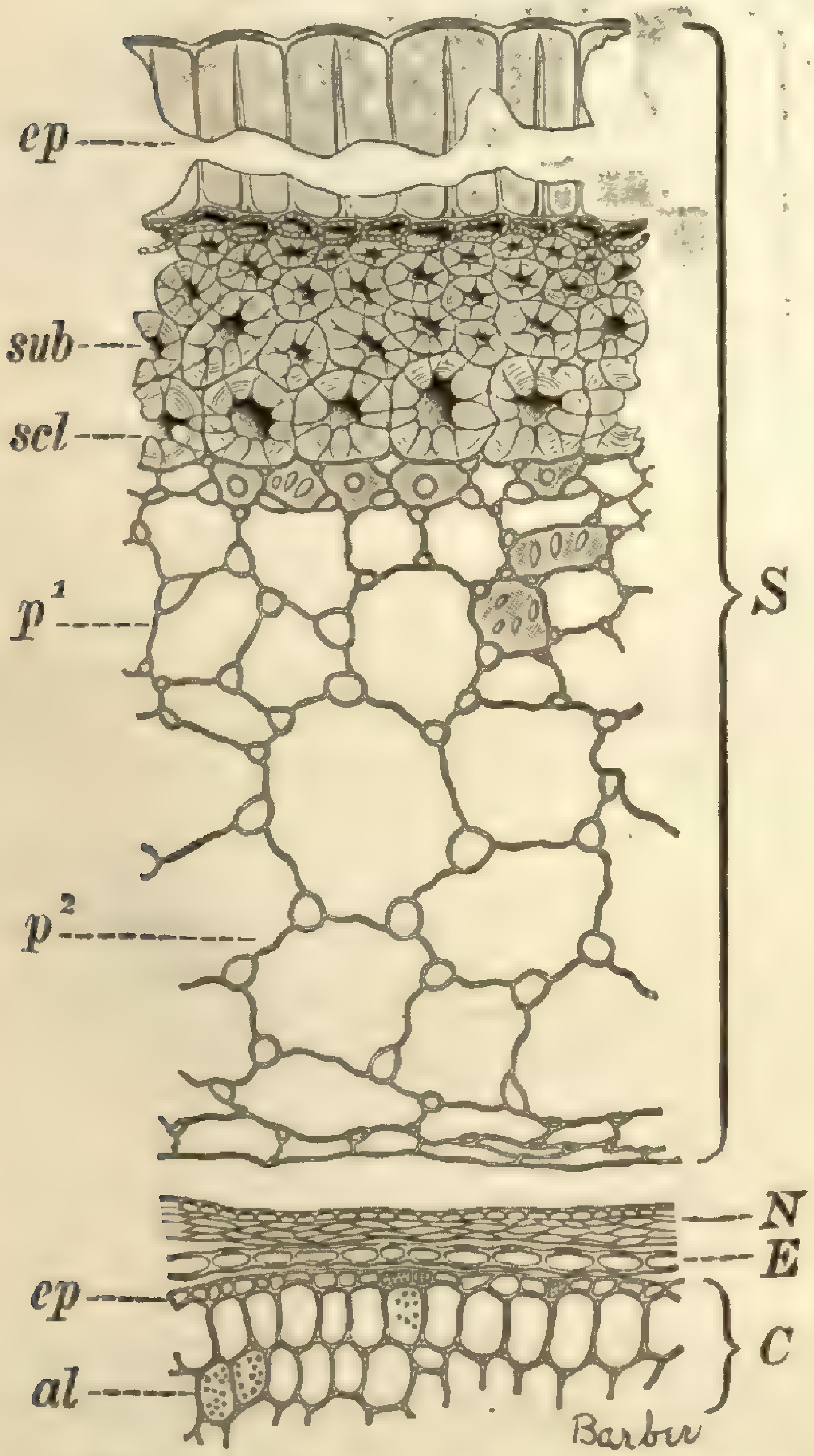


FIG. 19.—*Cucumis Melo* L. Isolated sclerenchyma cell of spermoderm. ×300.

3. *Sclerenchyma* (*scl* and *fig.* 19).—This single cell layer differs from that of *C. sativus* only in the irregular contour of the outer surface, where the layer conforms to the shape of the inner surface of the preceding layer.

4. *Parenchyma* (p^1 and p^2).—Beneath the sclerenchyma are one, sometimes two, layers of small cells, which are thin-walled, sclerenchymatized, and frequently pitted. This tissue gradually changes from without inward to larger-celled parenchyma with larger intercellular spaces.

5. *Inner epidermis.*—A layer of small parenchyma cells makes up this layer.

PERISPERM (*fig. 18, N*), ENDOSPERM (*fig. 18, E*), and EMBRYO (*fig. 18, C*) have the same structure as the corresponding parts in *C. sativus.*

CUCUMIS ERINACEUS L.

The seed of *Cucumis erinaceus* L. (*fig. 20*) is 6–8^{mm} long, 2–3^{mm} broad, and 1–1.5^{mm} thick, flattened, pointed, smooth, and yellow.

FIG. 20.—*Cucumis erinaceus* L. Seed. ×1.

SPERMODERM (*fig. 21*).—This is quite similar to that of *C. Melo.*

1. *Epidermis* (*ep*).—The prismatic cells are radially elongated to 70 μ, increasing in length but slightly if at all over the edge. Each radial wall has one rod broadened at the base and bluntly pointed at the outer end.

2. A *subepidermal layer* (*sub*), about six cells thick, consists of small, tangentially elongated cells, increasing in size over the edge of the seed. They are thick-walled, pitted, striated, and increase in size from without inward. Occasional small intercellular spaces are seen, especially at the edge.

3. *Sclerenchyma* (*scl*).—This single-celled layer, 40 μ in width, differs from the subepidermal layer principally in the greater size of the cells, which are longitudinally elongated and have very thick sinuous walls containing pits.

4. *Parenchyma* (*p*).—The outer layer is made up of very small cells with thin walls and small pits seen only with very high magnification. In the middle layers the cells are somewhat larger, also thin-walled, with intercellular spaces at the angles of the cells.

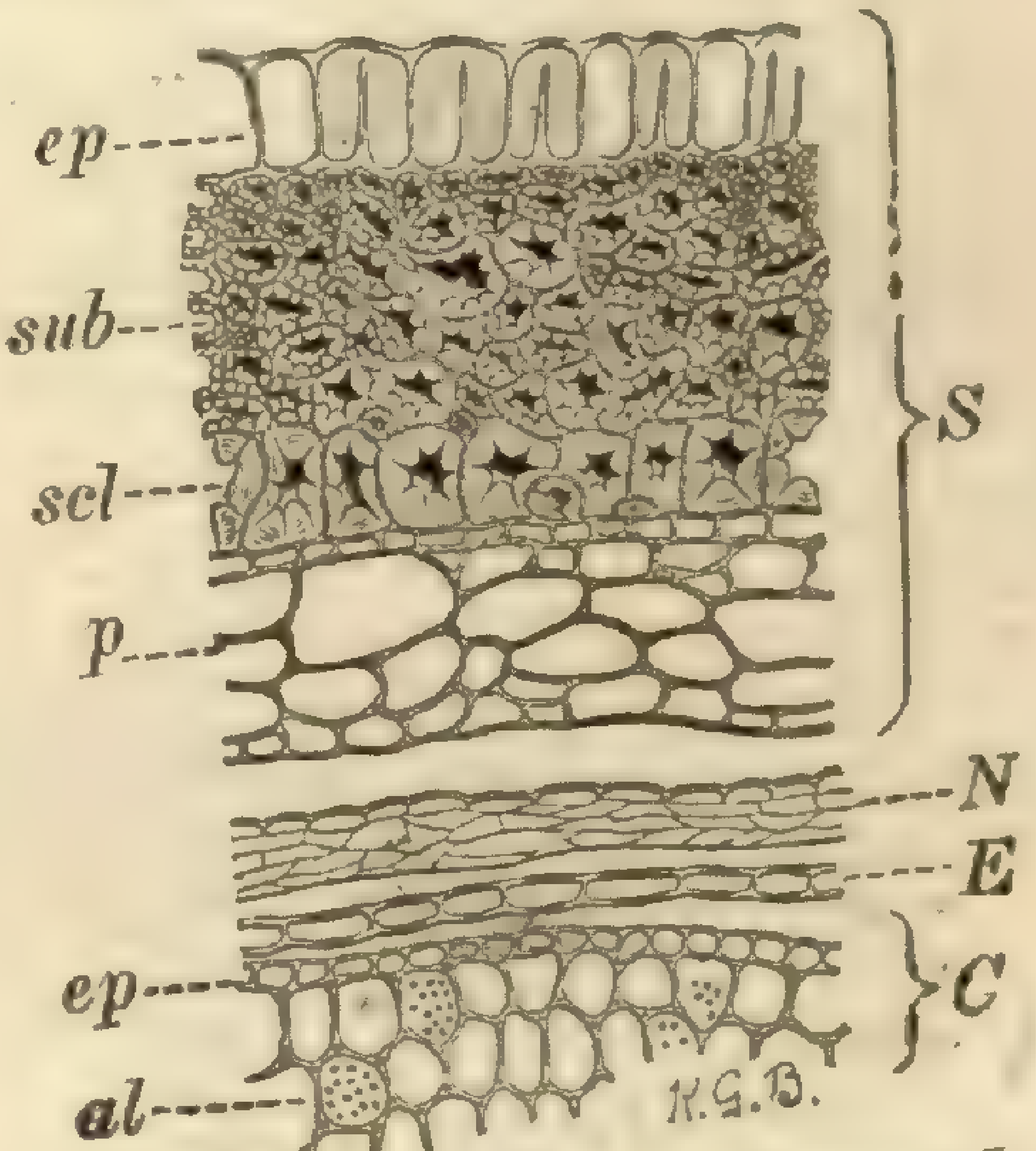


FIG. 21.—*Cucumis erinaceus* L. Seed in cross-section; *S*, spermoderm consisting of *ep*, ribbed palisade epidermis, *sub*, subepidermal layer, *scl*, sclerenchyma layer, *p*, parenchyma; *N*, perisperm; *E*, endosperm; *C*, cotyledon, consisting of *ep*, epidermis, and mesophyll with *al*, aleurone grains. ×160.

5. The *inner epidermis* consists of one layer of very small parenchyma cells.

PERISPERM (*fig. 21*, *N*), ENDOSPERM (*fig. 21*, *E*), and EMBRYO (*fig. 21*, *C*) present no new features.

CITRULLUS VULGARIS SCHRAD.

Citrullus vulgaris Schrad. (watermelon), now extensively cultivated in the tropics and warmer regions of the temperate zone, is a native of South Africa. ENGLER and PRANTL emphasize the fact that on its native soil the fruit forms a considerable part of the food of both the natives and the larger animals. This view is substantiated by LIVINGSTONE in his *Travels in Central Africa*.

The fruit is spherical, or more often ellipsoidal, of a dark green color, frequently mottled with white in ragged, longitudinal stripes several centimeters in width. The rind is firm but not hard, green at the outer surface, white further inward, changing gradually to the glistening pink, red, or yellow inner fruit-flesh, which contains 91–95 per cent. of water.

In the inner colored fruit-flesh are imbedded the numerous white, brown, or black mottled seeds (*fig. 22*). They are flat, without a border, lustrous, and smooth except when mottled, in which case they are slightly rough.

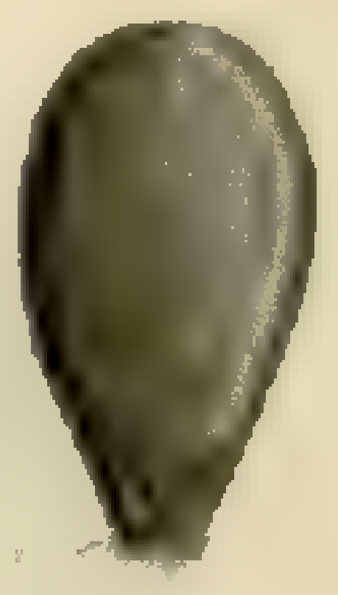


FIG. 22.—*Citrullus vulgaris* Schrad. Seed. ×1.

PERICARP (*figs. 23, 24*).—The great bulk of the fruit is the solid fruit-flesh, and it is this sweet, watery portion that is usually eaten and not the rind as in Cucurbita. The placentae are beautifully outlined, the bundles being of a somewhat lighter color than the flesh. When very ripe the flesh may separate along these lines, but no true cavity is formed. The individual cells of the inner flesh are visible to the naked eye.

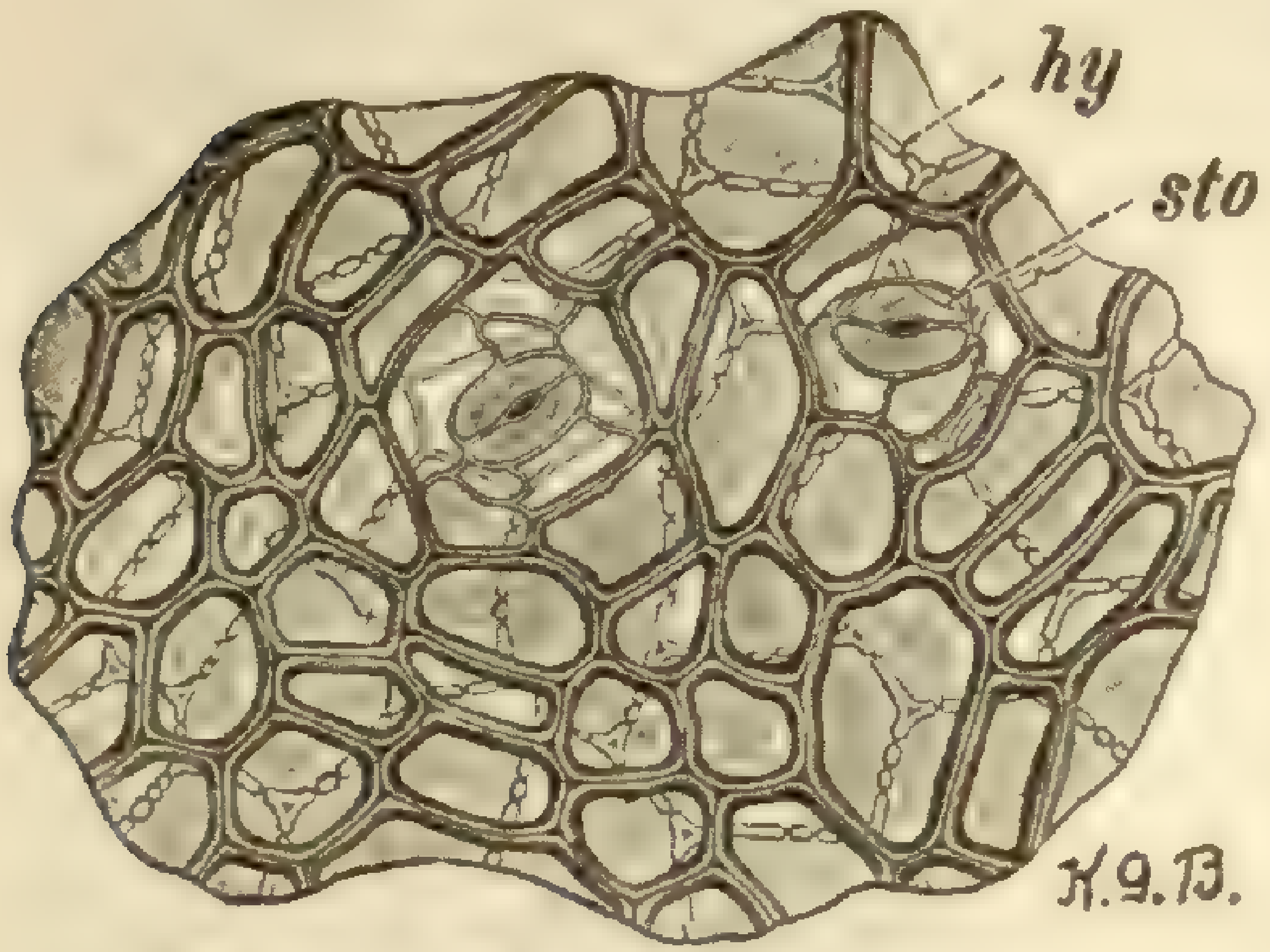


FIG. 23.—*Citrullus vulgaris* Schrad. Pericarp in surface view. Epicarp with *sto*, stoma; *hy*, hypoderm. ×160.

1. *Epicarp* (*epi*).—Instead of the true palisade cells there is a

layer, 33 μ in thickness, of cells often broader than high. The outer wall is very thick, the thickening running down on the radial walls. In surface view the middle lamella is visible and the hypoderm is quite evident through the thick-walled but transparent epicarp.

The ovary and very young fruit bear jointed hairs, which often reach a length of 32mm but are only 84 μ broad. They are borne on stalks of several joints, the foot becoming no larger than the surrounding epidermal cells in which it is imbedded. All the walls are only slightly thickened. These hairs disappear soon after fertilization, leaving scars which are evident only on the immature fruit.

Stomata (*sto*) are very numerous, occurring singly or in groups. They have rather large guard cells and thin-walled accompanying cells.

2. *Hypoderm* (*hy*).—A layer, many cells thick, containing chlorophyll, forms the green tissue of the rind. The outer layer consists of short cells, resembling those of the epicarp in size and shape; the following layers are made up of cells smaller in size and isodiametric. Numerous pits are present, the walls appearing distinctly beaded in surface view. Small intercellular spaces occur throughout the tissue.

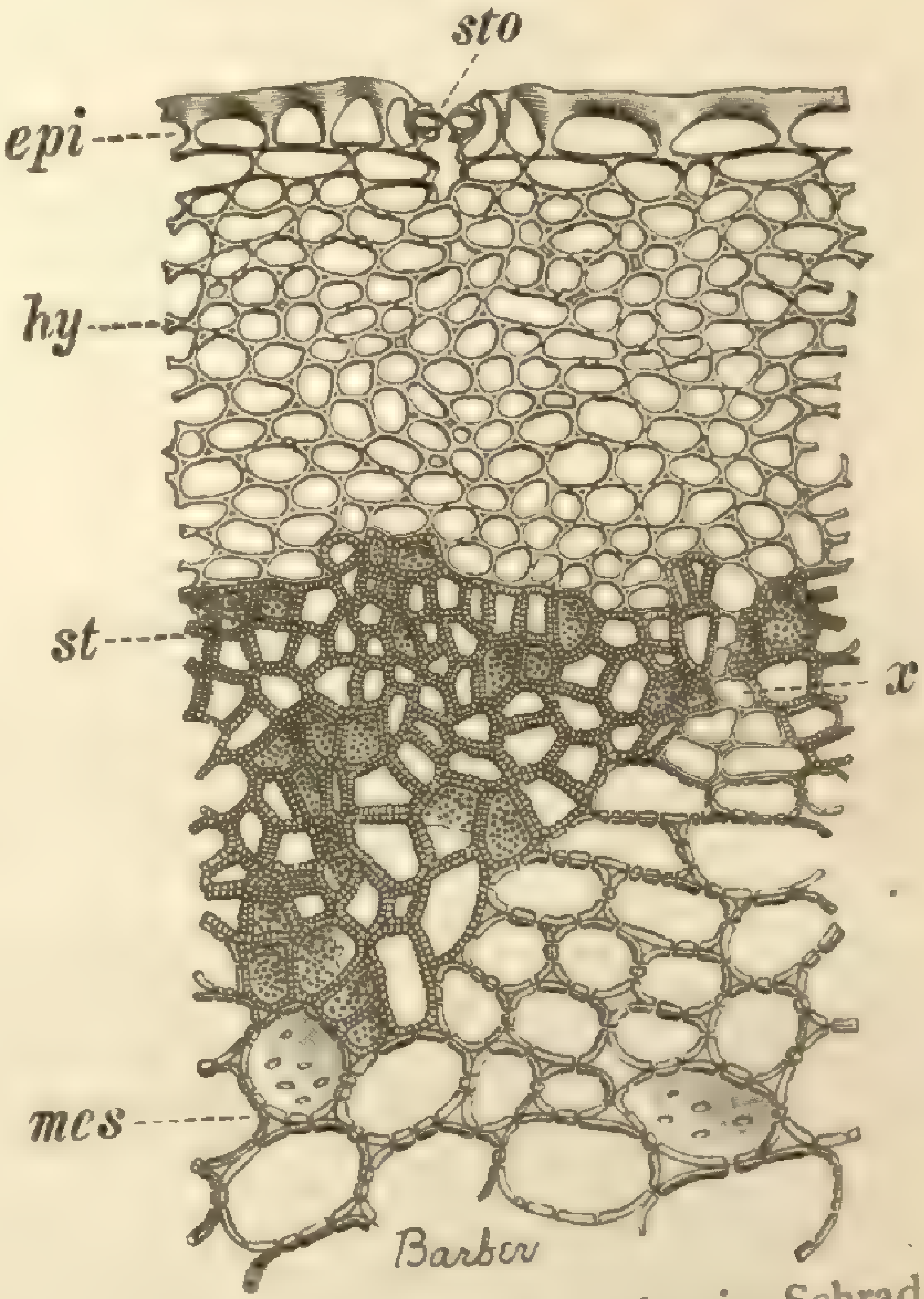


FIG. 24.—*Citrullus vulgaris* Schrad. Pericarp in cross-section; *epi*, epicarp with *sto*, stoma; *hy*, hypoderm; *st*, outer mesocarp (stone-cell layer); *x*, parenchyma between groups of stone cells; *mes*, middle mesocarp. ×160.

3. *Outer mesocarp* (*st*).—In the very young fruit the cells are small and isodiametric, but after a few weeks single cells or groups of cells thicken their walls and become pierced with pits. These groups are distributed about the fruit just within the hypoderm. As growth of the fruit continues, these cells increase in number, the groups

approaching each other until there is eventually, in the mature fruit, a distinct zone of stone cells surrounding the inner tissues. This stone-cell layer is not quite continuous, the groups being separated in many places by a few cells which retain their thin cellulose walls and afford easy communication between the hypoderm and middle mesocarp (*x*). The inner contour of the layer is very irregular.

4. *Middle mesocarp* (*mes*).—The cells are thickened, pitted, and gradually increase in size from the small outer layers inward.

5. *Inner mesocarp.*—This layer is the great central mass of pink (or yellow) tissue. The cells are of enormous size, often 1.25^{mm} in diameter, and, as previously stated, they can be easily distinguished with the naked eye. The walls are thin and are separated at the angles by intercellular spaces. A sweet, watery liquid fills the cavity.

Bundles, sieve tubes, and latex tubes are found scattered throughout the mesocarp.

6. The *endocarp* consists of one layer of small, very thin-walled, elongated cells as in *C. sativus*.

SPERMODERM (*fig. 25*).—This coat, consisting of the usual number of layers, is thin but very firm.

1. *Epidermis* (*ep*).—Prismatic cells form a palisade layer covered with a thick cuticle, which occasionally reaches a thickness of 35μ. The outer and inner walls have wavy contours, that of the inner wall being much more pronounced. Each radial wall, which is thicker than in the species previously described, has one thickening in the form of a straight rod pointed at the outer end. Occasionally it branches once dichotomously, the two branches running straight out to the cuticle. These rods are sclerenchymatized, responding to the test with iodin and sulfuric acid. In the colored seeds the brown or mottled appearance is due to the colored contents of the epidermal cells.

2. The *subepidermal layer* (*sub*) consists of a number of layers of sclerenchymatized cells, increasing in number over the edges. The outer cells are small and isodiametric; those of the middle layers, large and radially elongated; while the inner cells are noticeably small. The cell walls increase in thickness from without inward, those of the inner layer having scarcely any cell cavities. All of the walls are sinuous and deeply pitted.

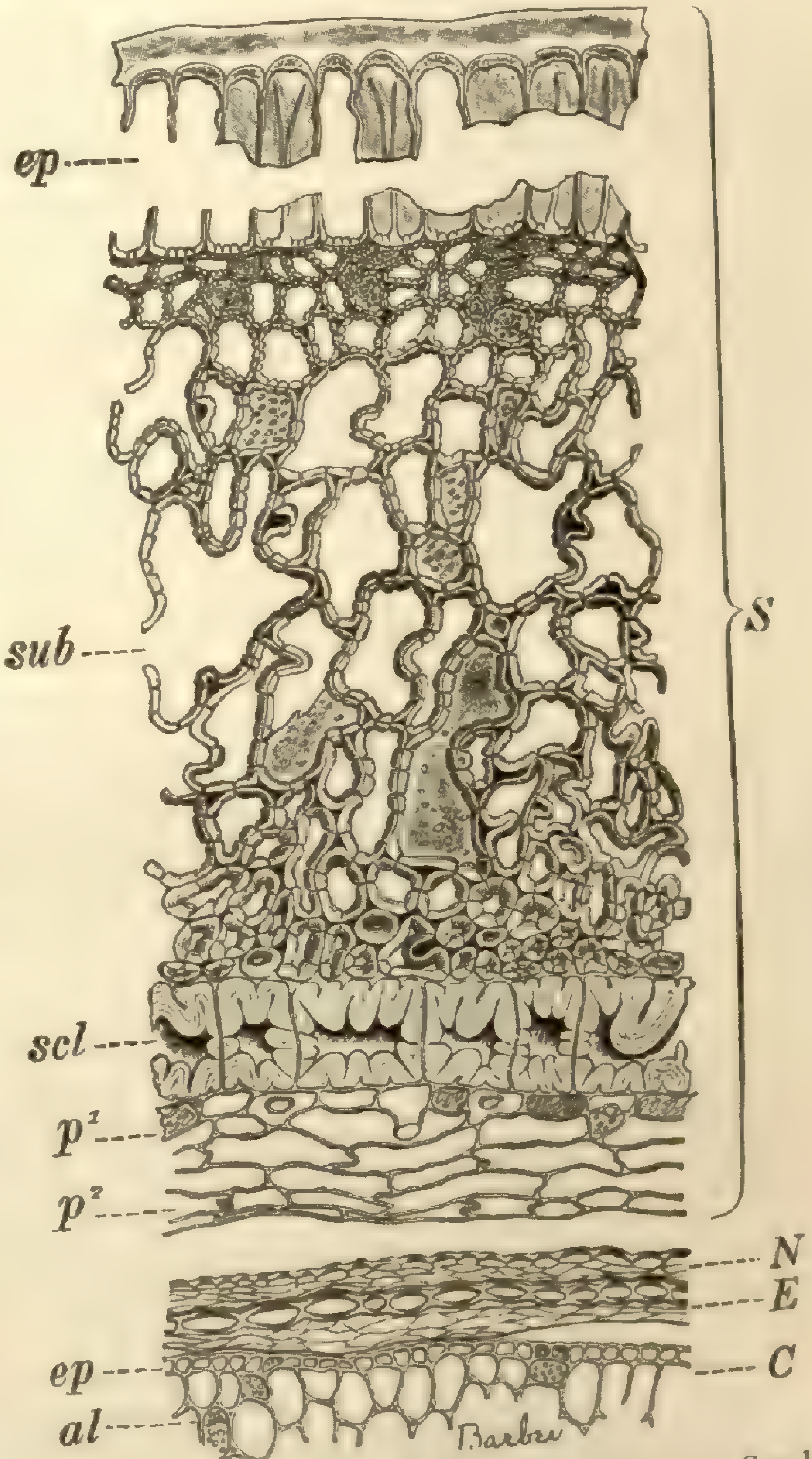


FIG. 25.—*Citrullus vulgaris* Schrad. Seed in cross-section; *S*, spermoderm consisting of *ep*, epidermis, *sub*, subepidermal layer, *scl*, sclerenchyma, p^1, sclerenchymatized parenchyma, p^2, inner parenchyma; *N*, perisperm; *E*, endosperm; C, cotyledon, with *ep*, epidermis, and mesophyll, containing *al*, aleurone grains. ×160.

3. *Sclerenchyma* (*scl*).—This layer differs somewhat from the corresponding layer of the other cucurbitaceous seeds. Instead of conspicuously elongated cells arranged end to end in rows, they are but slightly if at all elongated and very irregularly distributed, showing only the faintest indications of an end-to-end arrangement. In other respects, that is as regards thickness and sinuosity of the pitted walls, they are similar.

4. *Parenchyma.*—One layer of small and somewhat spongy cells forms the outer tissue (p^1). They are thin-walled, pitted, and sclerenchymatized. Below are several other layers of more or less spongy parenchyma, the cells decreasing in size toward the inner epidermis (p^2).

5. *Inner epidermis.*—This layer consists of small, thin-walled cells.

PERISPERM (*fig.* 25, *N*).—An epidermis of longitudinally elongated cells with a cuticle covers a number of layers of thin-walled parenchyma.

ENDOSPERM (*fig.* 25, *E*).—This is the only species studied in which this layer is more than one cell thick. In *Echinocystis lobata* there are occasional broken-down cells below the thick-walled protein layer, but in the present species the cell layers are numerous, forming a tissue as thick as the perisperm. The outer polygonal cells are of the kind described for other species, and the inner layers consist of extremely thin-walled parenchyma, distinguishable only after treatment with Javelle water.

The EMBRYO (*fig. 25, C*) corresponds to that of the general description.

SICYOS ANGULATUS L.

Sicyos angulatus L. is a native of northeastern United States, occurring as a weed in damp places, and is also occasionally cultivated for arbors.

The fruits, each consisting of a small ovate pericarp (up to 2^{cm} in length), filled with a single seed, are borne in capitate clusters on a long peduncle. They are dry and covered with deciduous barbed prickles, $8-10^{mm}$ long, which give them a burrlike appearance.

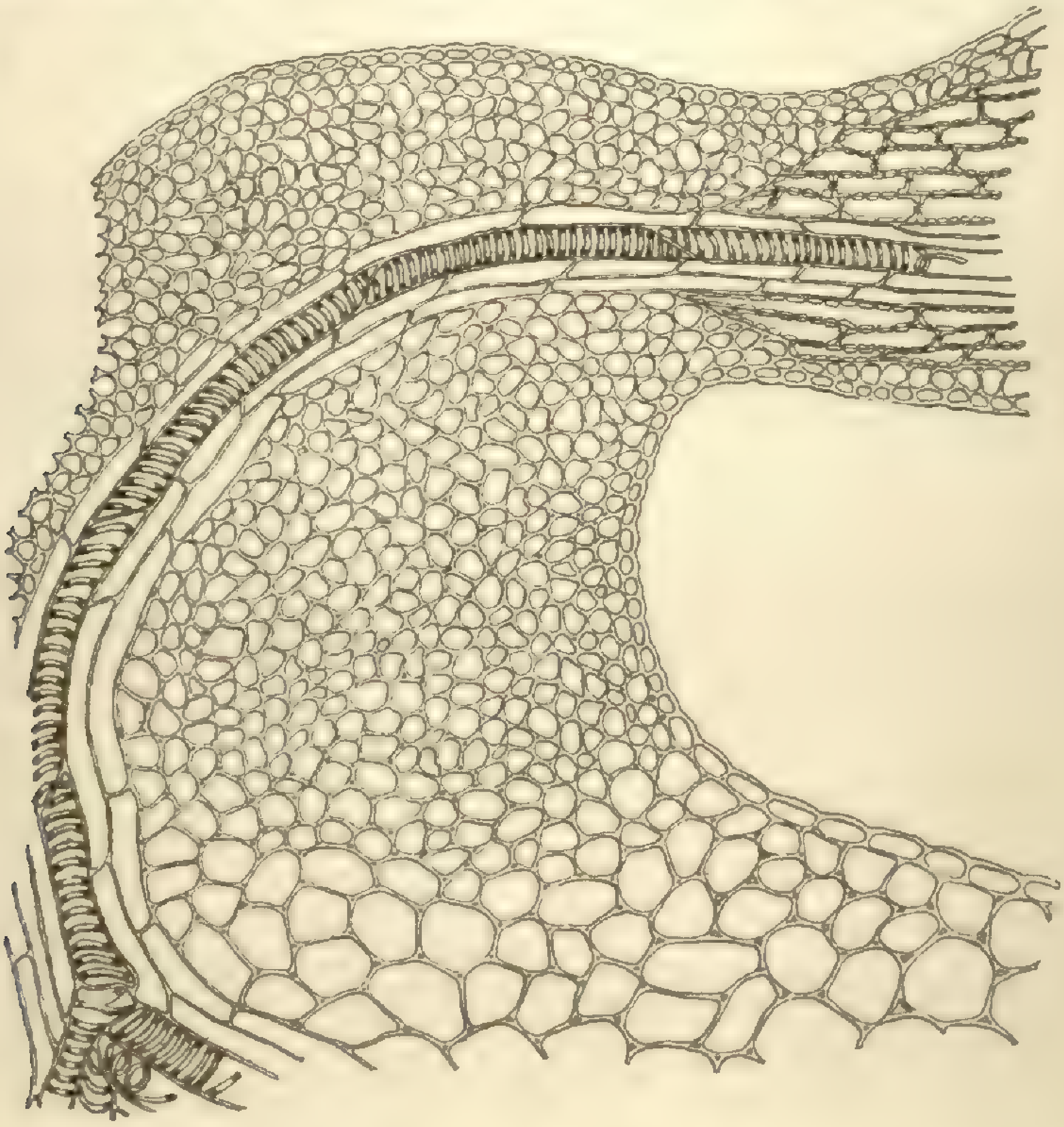


FIG. 26.—*Sicyos angulatus* L. Base of prickle in cross-section, showing characteristic small cells. ×160.

The brown seeds are 12^{mm} in length and 10^{mm} broad, flattened, ovate, smooth, and lustrous.

PERICARP (*figs. 26–29*).—This coat forms only a very thin covering for the seeds and does not make up the bulk of the fruit, as in the other species described. The surface is roughened and covered with spines and hairs, of which, as described below, there are four forms.

1. *Epicarp.*—This layer is composed of small flattened cells 13 μ high, with slightly thickened walls. In surface view they are polygonal and 20 μ in diameter (*fig. 29*).

Very striking are the prickles (emergences), each being a long (8-10^{mm}) outgrowth borne on a swelling of the pericarp (*fig. 26*). They have a constricted base, the epidermis of which consists of thin-walled cells. Above this base the epidermal cells elongate and become thickened. Over all the surface of the prickles are borne slightly curved, single-celled, conical hairs (often 135 μ in length), with extremely thick walls (*fig. 27*). They are very stiff and turn sharply backward. Doubtless they play an important part in the dispersal of the seeds, acting as barbs to fasten securely the prickles, and thereby the fruit, to passing animals. Similar pointed but not deflexed hairs occur on the epicarp, either singly or in pairs.

At the end of the prickle there is a thin-walled capitate hair, consisting of a stalk of several short cells and a single-celled glandular head (*fig. 27*).

Among the prickles there are also large glandular hairs, reaching a length twice that of the emergence (*figs. 28, 29*, t^1). The foot consists of one or two enlarged epidermal cells and is surrounded by cells but slightly smaller. From the foot the cells are elongated and thin-walled, the hair tapering gradually and ending with short glandular cells. The prickles become entangled in the hairs and do not fall off, even though detached from the pericarp.

Another form of hair (*fig. 29*, t^2) on the pericarp is thin-walled, unicellular or several-jointed, reaching a maximum length of 540 μ. The end cell is conical and not glandular as in the preceding hair.

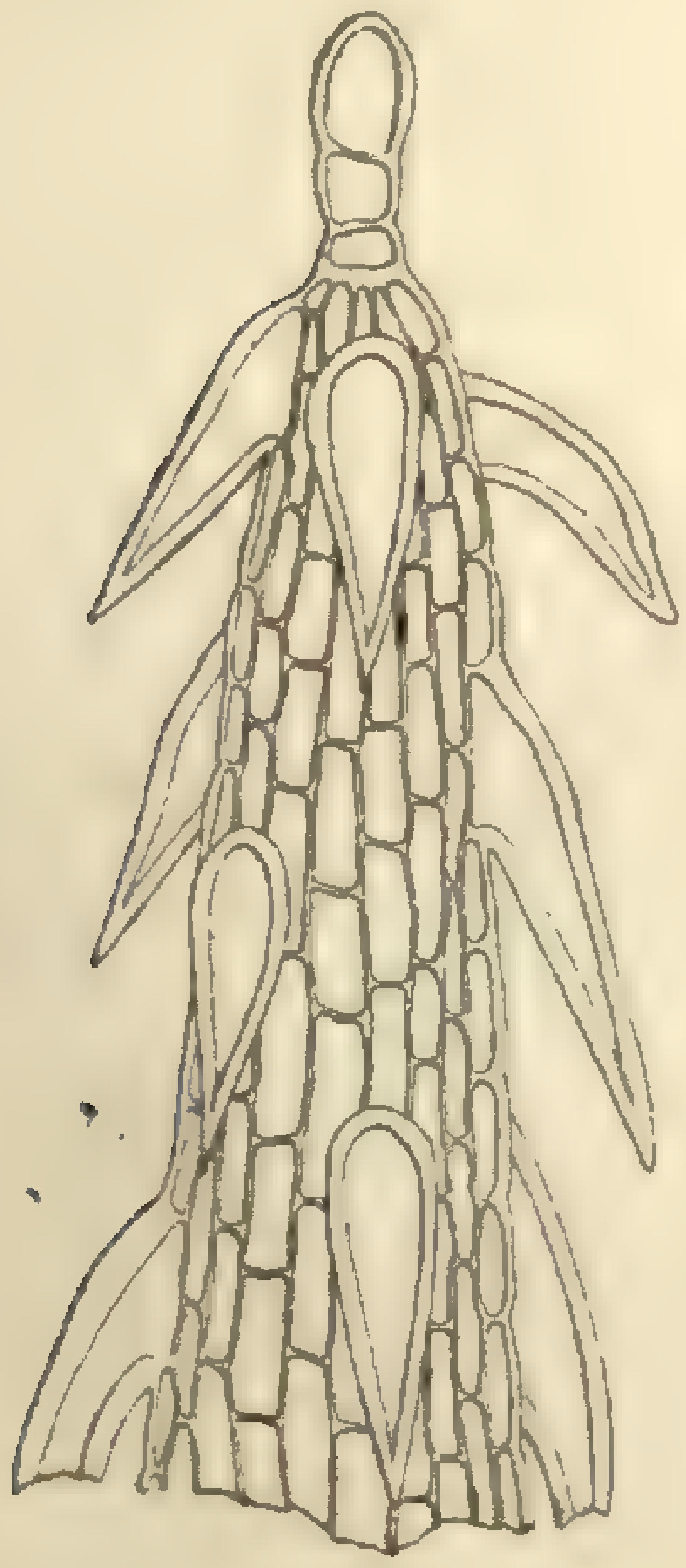
Numerous stomata occur among these hairs.

2. *Hypoderm.*—One or more layers of very small isodiametric cells form an inconspicuous layer just within the epicarp. The hypodermal cells of the constricted base of the prickle are also very minute and thin-walled. These together with the thin-walled epidermis permit the prickle to be readily detached at maturity. In the prickle the cells are elongated and sclerenchymatized, with numerous pits (*fig. 26*).

3. *Outer mesocarp.*—Several rows of small rounded cells with intercellular spaces make up this tissue. In the vicinity of the prickles and hairs they are sclerenchymatized and tangentially elongated.

4. The *middle mesocarp* consists of several layers of large-celled, loosely arranged parenchyma with intercellular spaces.

5. *Inner mesocarp.*—The cells of this coat, although somewhat smaller than those of the middle mesocarp, form several layers of similar tissue.



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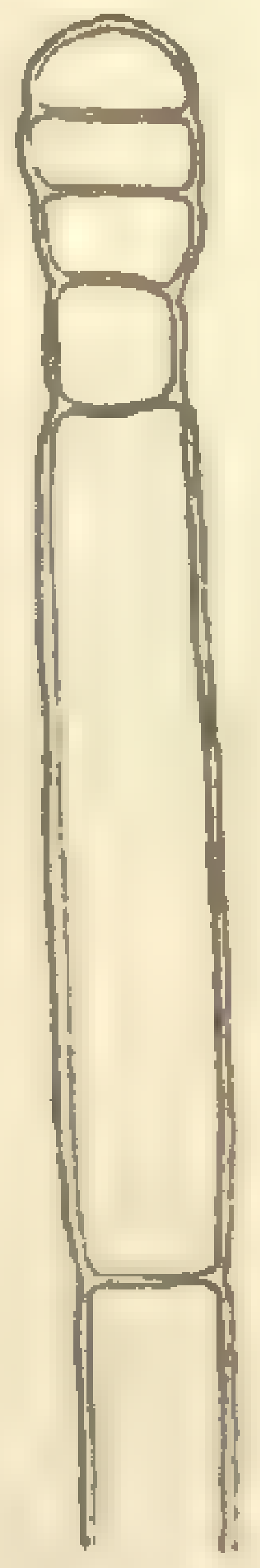

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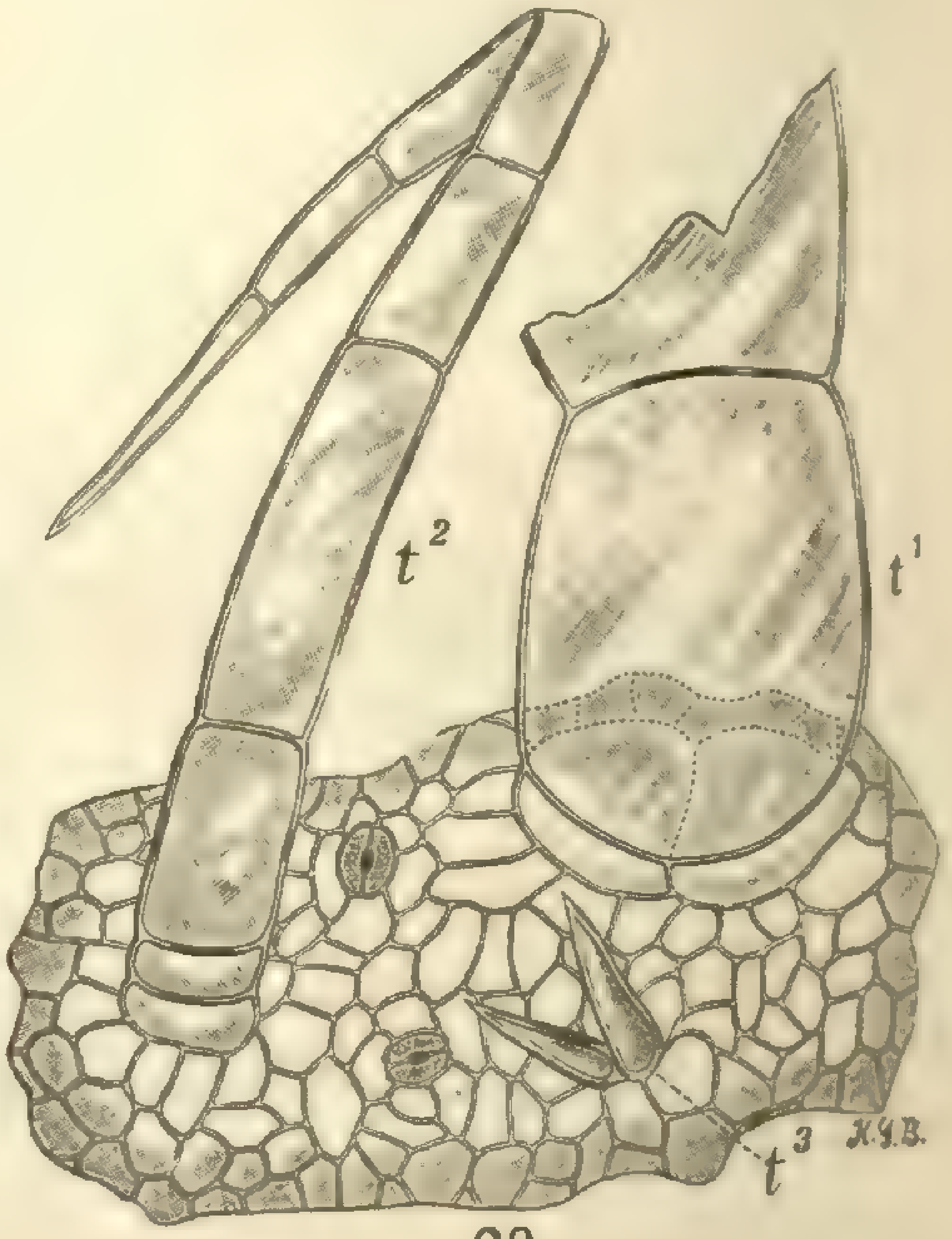

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FIG. 27. *Sicyos angulatus* L. Apex of spine. × 160.—FIG. 28. *Sicyos angulatus* L. Apex of long jointed hair. × 160.—FIG. 29. *Sicyos angulatus* L. Epicarp in surface view; t^1, base of glandular hair; t^2, short pointed conical hair; t^3, unicellular conical hair. × 160.

The bundles and latex tubes, few in number, are scattered through the mesocarp.

6. *Endocarp.*—As in *Cucurbita Pepo*, the single layer of longitudinally elongated, thin-walled cells remains on the seed.

SPERMODERM (*fig. 30*).—1. *Epidermis* (*ep*). Prismatic cells form a palisade layer only 50 μ in width. In cross-section no thickenings are apparent on the radial walls, but in surface view, what appeared in the cross-section to be walls thickened at the angles are rods running, one on each wall, from the inner to the outer wall which they seem to join. No cuticle is present; the thickening, however, is continued on the inner wall.

2. *Subepidermal layer* (*sub*).—Small thin-walled cells, 13 μ in diameter, with intercellular spaces, make up one layer. Additional cells of the same type are present below the radial walls of the epidermis, making the tissue two cells thick in those places.

3. *Sclerenchyma* (*scl*).—As in Echinocystis, there is one layer of radially elongated cells forming a palisade layer, 230 μ in width, which is best seen in cross-section. The cell cavities are narrow, constricted about 70 μ from the outer wall, from which constriction branches radiate toward the outer wall. This is repeated at the other end, the constriction being slightly nearer the inner wall. In surface view the cells are sinuous and indefinitely arranged.

4. *Parenchyma.*—The outer cells are small and thin-walled (p^1) and the several middle layers consist of large stellate cells and intercellular spaces (p^2). All of these layers are sclerenchymatized. About ten layers of spongy parenchyma, the cells decreasing in size inward, form the inner tissues (p^3). These cells contain chlorophyll, which gives the tissue a distinct green color.

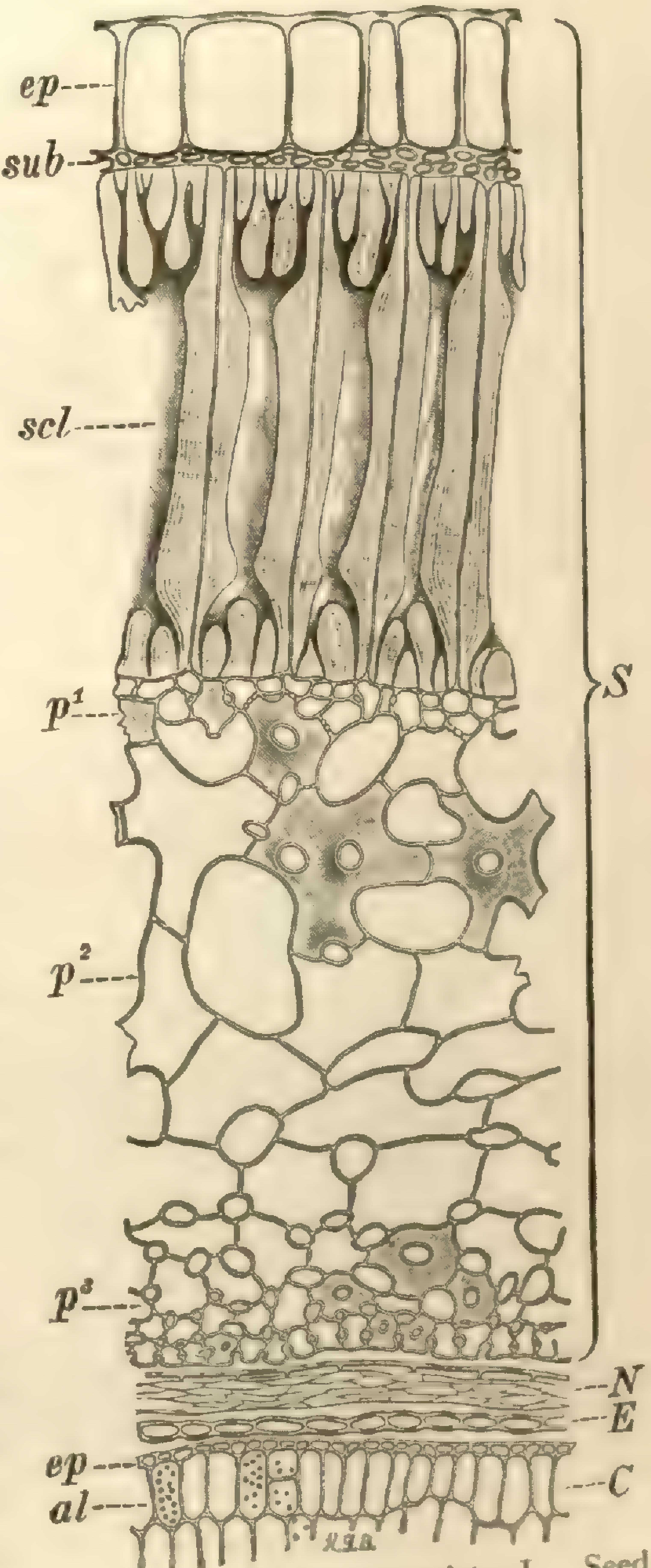


FIG. 30.—*Sicyos angulatus* L. Seed in cross-section; *S*, spermoderm consisting of *ep*, epidermis, *sub*, subepidermal layer, *scl*, sclerenchyma, p^1, small-celled outer parenchyma, p^2, large-celled spongy parenchyma, p^3, small-celled spongy parenchyma; *N*, perisperm; *E*, endosperm; *C*, cotyledon with *ep*, epidermis, and mesophyll containing *al*, aleurone grains. ×160.

5. The *inner epidermis* with small, thin-walled cells resembles that of *Cucurbita Pepo*.

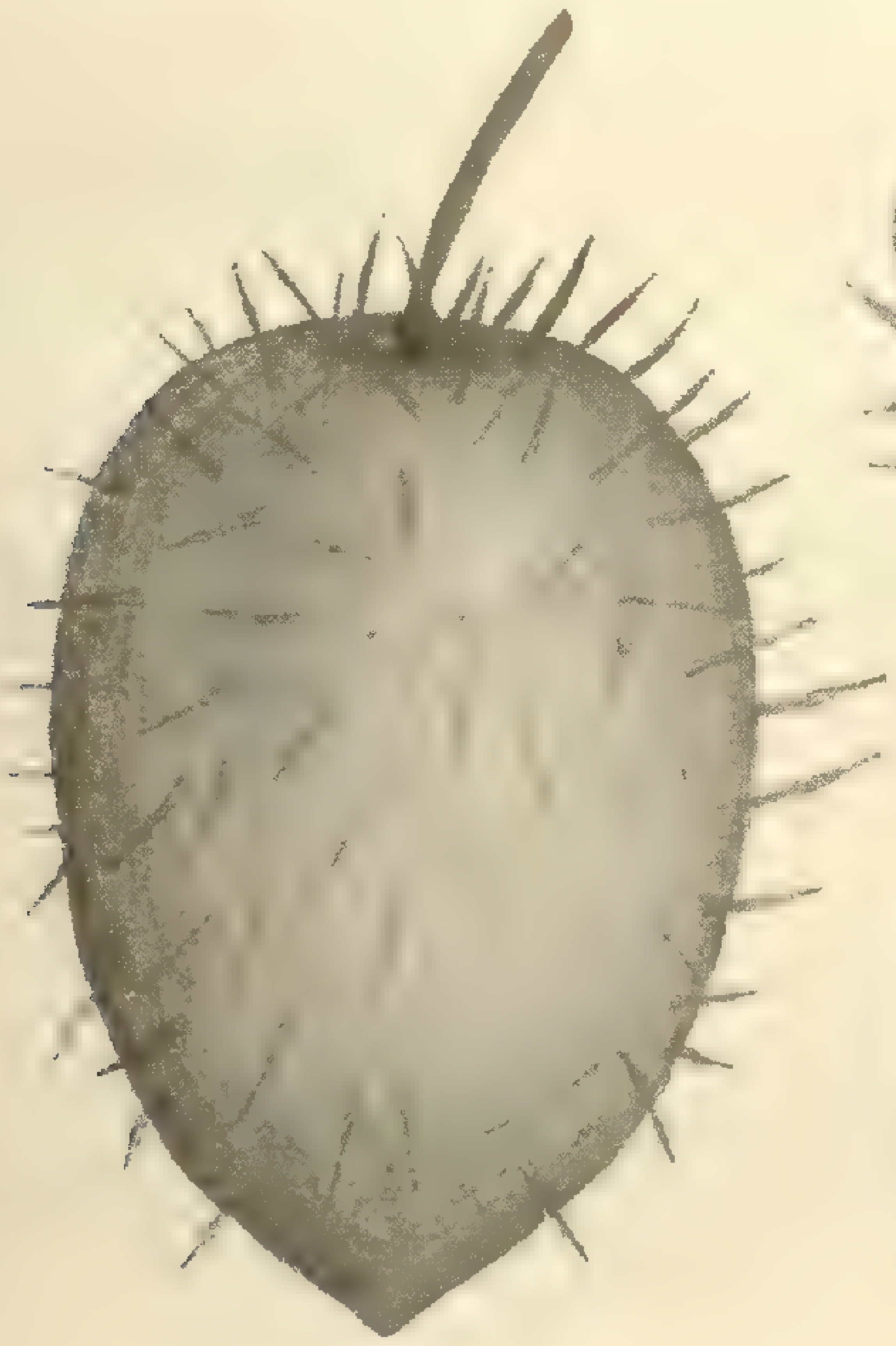
PERISPERM (*fig. 30, N*).—Five or six layers of parenchyma, with outer epidermis and cuticle, have the same structure as the corresponding layer of other species. The most characteritsic feature is the transversely elongated epidermal cells.

ENDOSPERM (*fig. 30, E*).—This consists of one layer of thick-walled cells containing protein granules.

EMBRYO (*fig. 30, C*).—No characteristic features are evident.

ECHINOCYSTIS LOBATA TORR. & GR.

This plant, *Echinocystis lobata* Torr. & Gr. (*Sicyos lobatus* Michx., *Momordica echinata* Muhl.), is one of the two Cucurbitaceae indigenous to New England. It has no value as a food, but is quite extensively cultivated for arbors.



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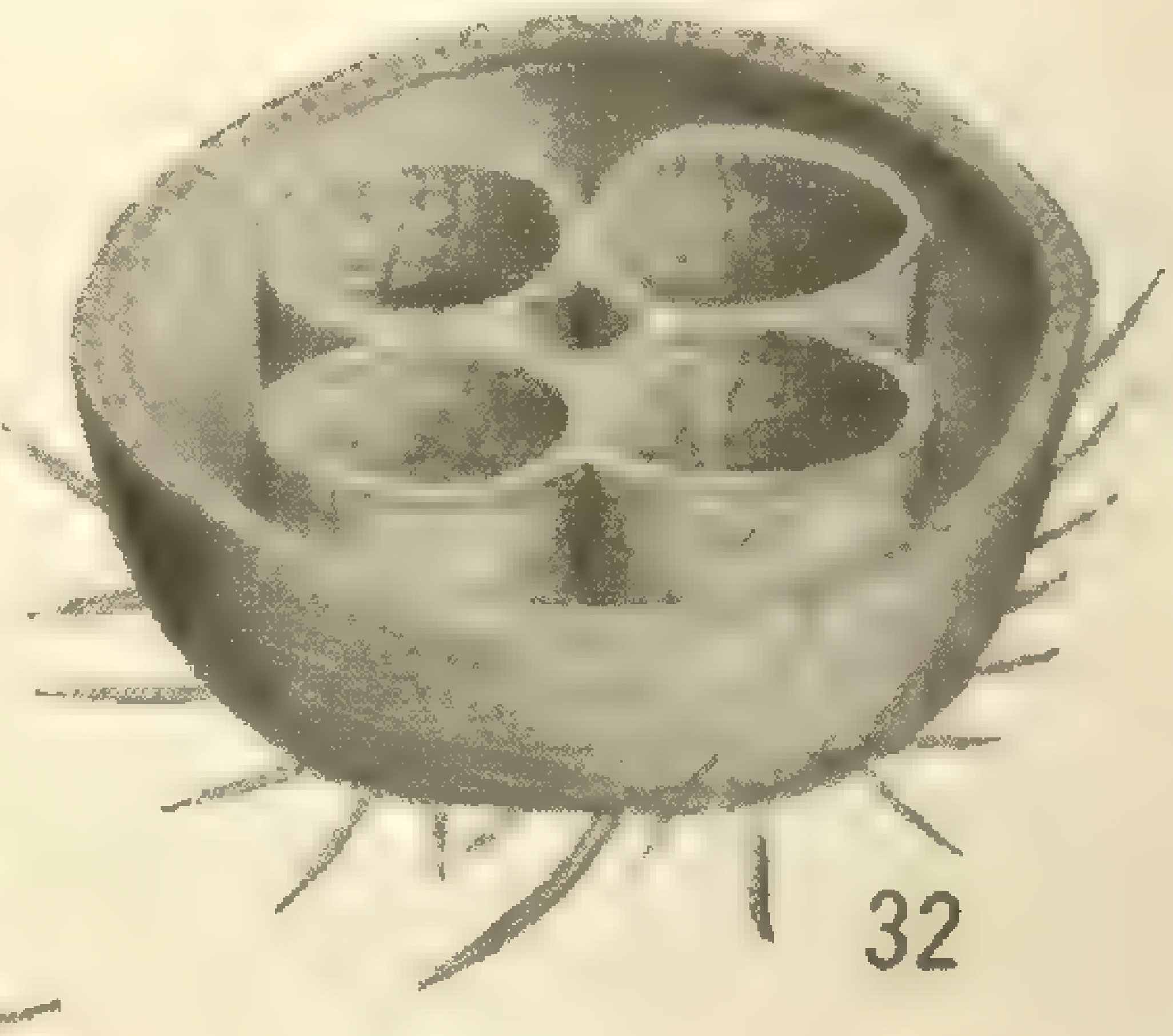

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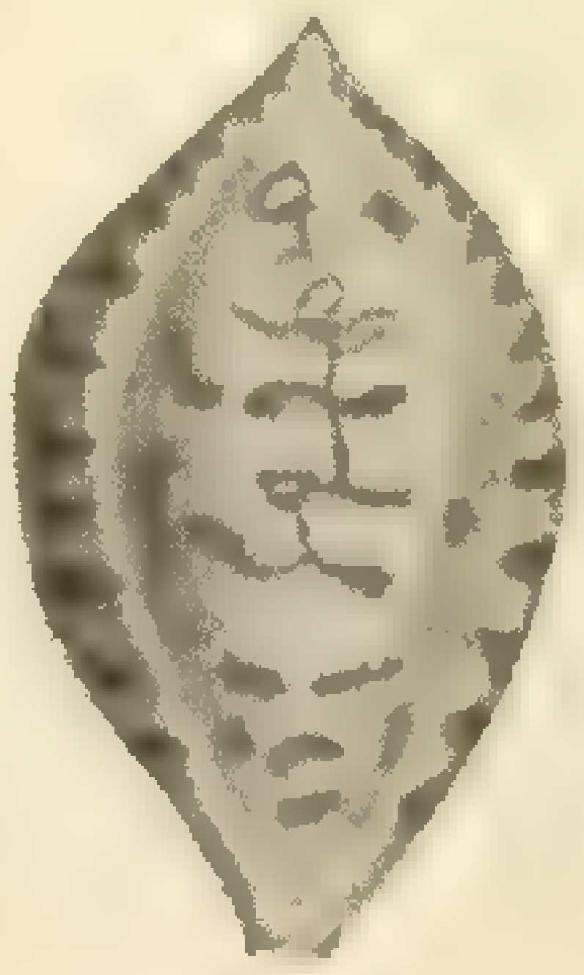

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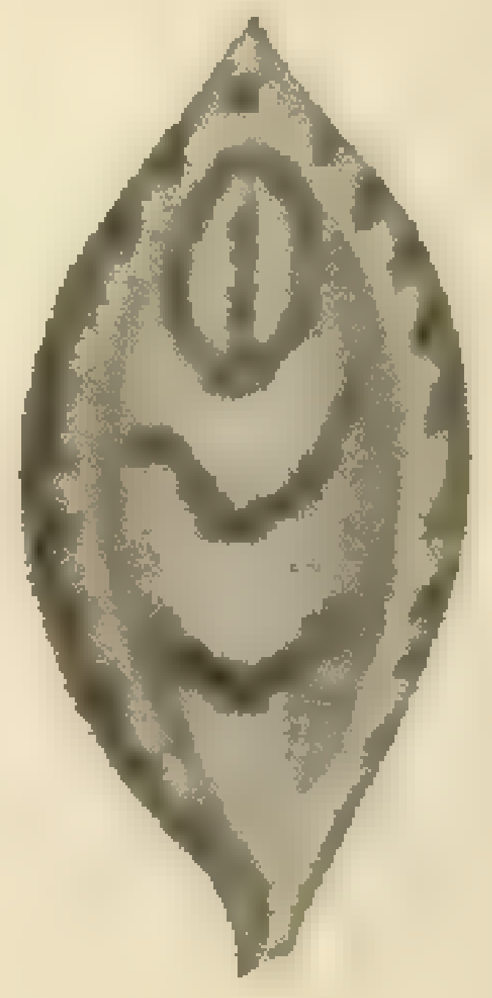

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FIG. 31. *Echinocystis lobata* Torr. & Gr. Fruit. ×1.—FIG. 32. *Echinocystis lobata* Torr. & Gr. Fruit in cross-section. ×1.—FIG. 33. *Echinocystis lobata* Torr. & Gr. Seed. ×1.—FIG. 34.—*Echinocystis lobata* Torr. & Gr. Seed. ×1.

The oval fruit (*fig. 31*) is 5^{cm} long, light green in color, and covered with soft spines 12^{mm} in length. At maturity it bursts irregularly at the top, showing the fruit-flesh separated into an outer and inner tissue consisting of a fibrous network. This inner part forms two large oblong cells, each divided at the base into two one-seeded locules, as shown in *fig. 32*. Soon after dehiscence the pod dries up.

The flattened ovate seeds are 20^{mm} in length, 8^{mm} broad, and 4^{mm} thick. The color is gray brown with beautiful brown markings (*figs. 33, 34*) varying greatly on different specimens. On the flattened surface of some seeds these markings are in the form of circles, on others as various shaped spots, but about the edge they generally form a border of elongated diagonally arranged blotches. The embryo differs from the typical embryo only in the greater thickness of the cotyledons.

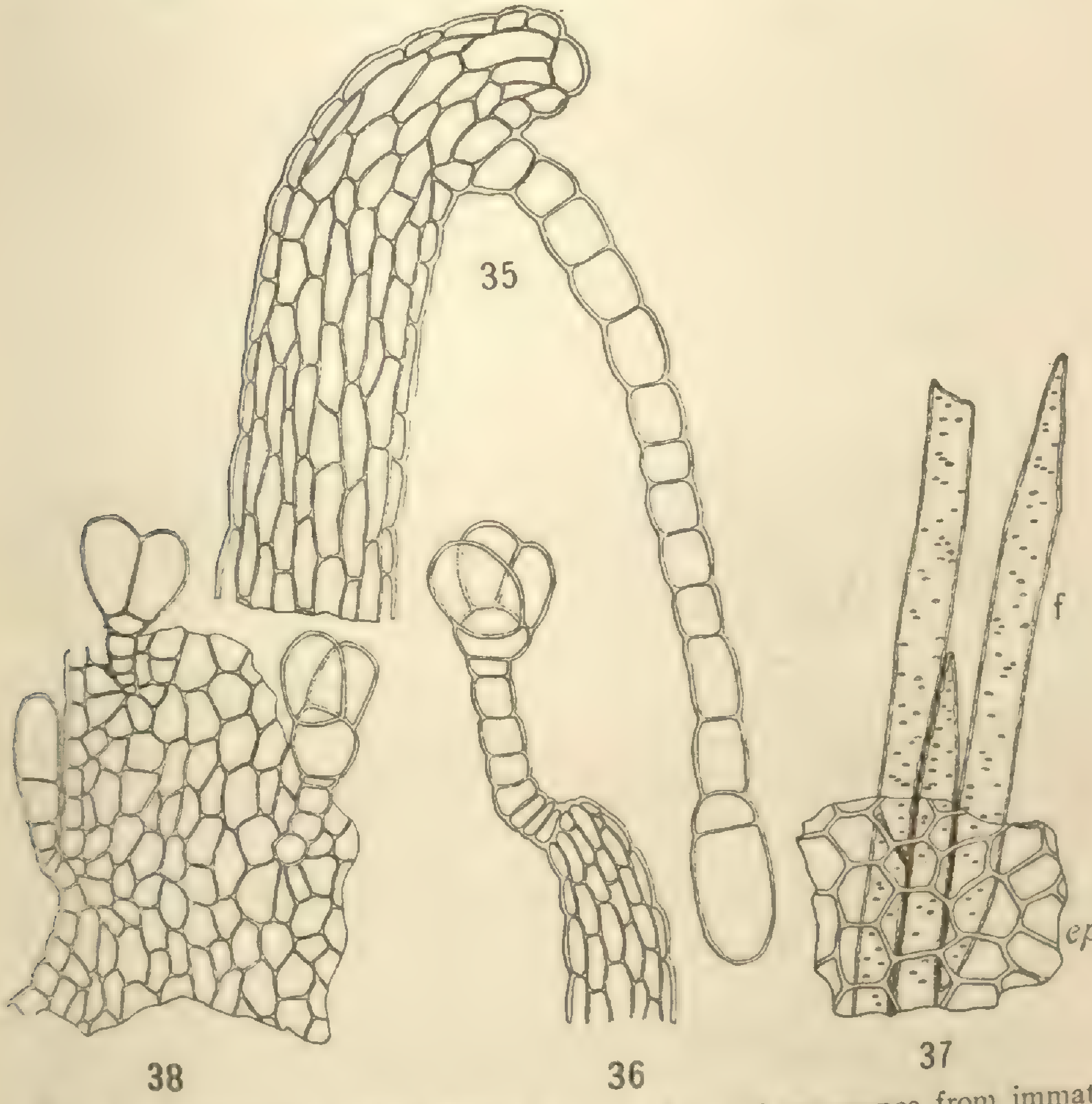


FIG. 35. *Echinocystis lobata* Torr. & Gr. Apex of emergence from immature pericarp. ×160.—FIG. 36. *Echinocystis lobata* Torr. & Gr. Apex of emergence from immature pericarp. ×160.—FIG. 37. *Echinocystis lobata* Torr. & Gr. Mature spine in surface view; *ep*, epidermis; *f*, fibers of hypoderm. ×160.—FIG. 38. *Echinocytis lobata* Torr. & Gr. Base of emergence from immature pericarp. ×160.

PERICARP (*figs. 35–39*).—The outer part, or prickly rind, consists of the epicarp and outer mesocarp, the inner of the hard, stiff bundles with only vestiges of ground tissue.

1. *Epicarp* (*figs. 37, 39*).—The cells of this layer are slightly thickened, in surface view appearing polygonal and distinctly beaded. On the spines the epidermal cells are elongated and have thick walls.

The tip of each spine (*figs. 35, 36*) curves decidedly, bearing at the very extremity, or more frequently just below it, a long, jointed, capitate hair. There is great variation among these hairs. They point downward, upward, or in an intermediate direction; the joints may be few or many, the length of the hair varying accordingly. Each cell is about as long as broad, with moderately thickened outer and slightly thinner cross walls. The head consists of one cell (*fig. 35*), two (*fig. 38*), arranged side by side, or three (*fig. 36*), arranged about a common axis. They have free rounded ends and are elongated, with longitudinal diameter twice that of the transverse.

Similar hairs, but much shorter, with one- to three-celled stalks, are present on the sides of the spine (*fig. 38*). All of the hairs frequently disappear before the fruit reaches maturity.

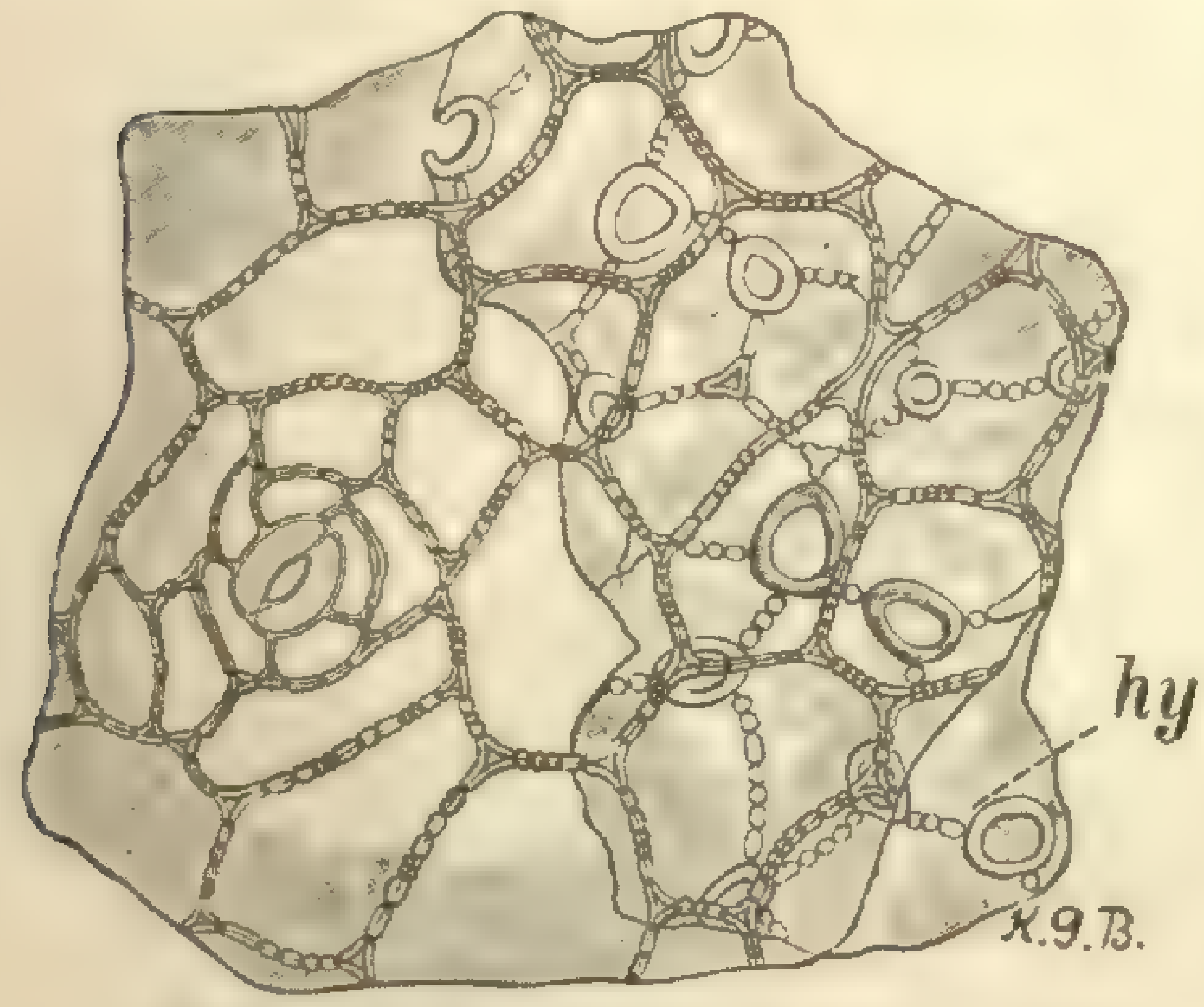


FIG. 39.—*Echinocystis lobata* Torr. & Gr. Pericarp in surface view; epicarp with *hy*, hypoderm. ×160.

Interspersed among the spines are the stomata with small pitted accompanying cells.

2. *Hypoderm* (*fig. 39, hy*).—Several layers of pitted cells make up this layer. They are polygonal, thick-walled, and have circular intercellular spaces at the angles, about which the walls are very thick. In the spines the walls are also thickened and pitted, and in addition very much elongated longitudinally. The hypoderm shows through the transparent epicarp, the circular intercellular spaces, with strongly thickened surrounding walls, being especially characteristic.

3. *Outer mesocarp.*—Several layers of isodiametric parenchyma cells form the tissue below the hypoderm. The cells are small and thin-walled.

4. The *middle mesocarp* cells are large, thin-walled, and mostly broken down in the mature fruit, thus forming the cavity between the outer rind and inner fibrous tissue.

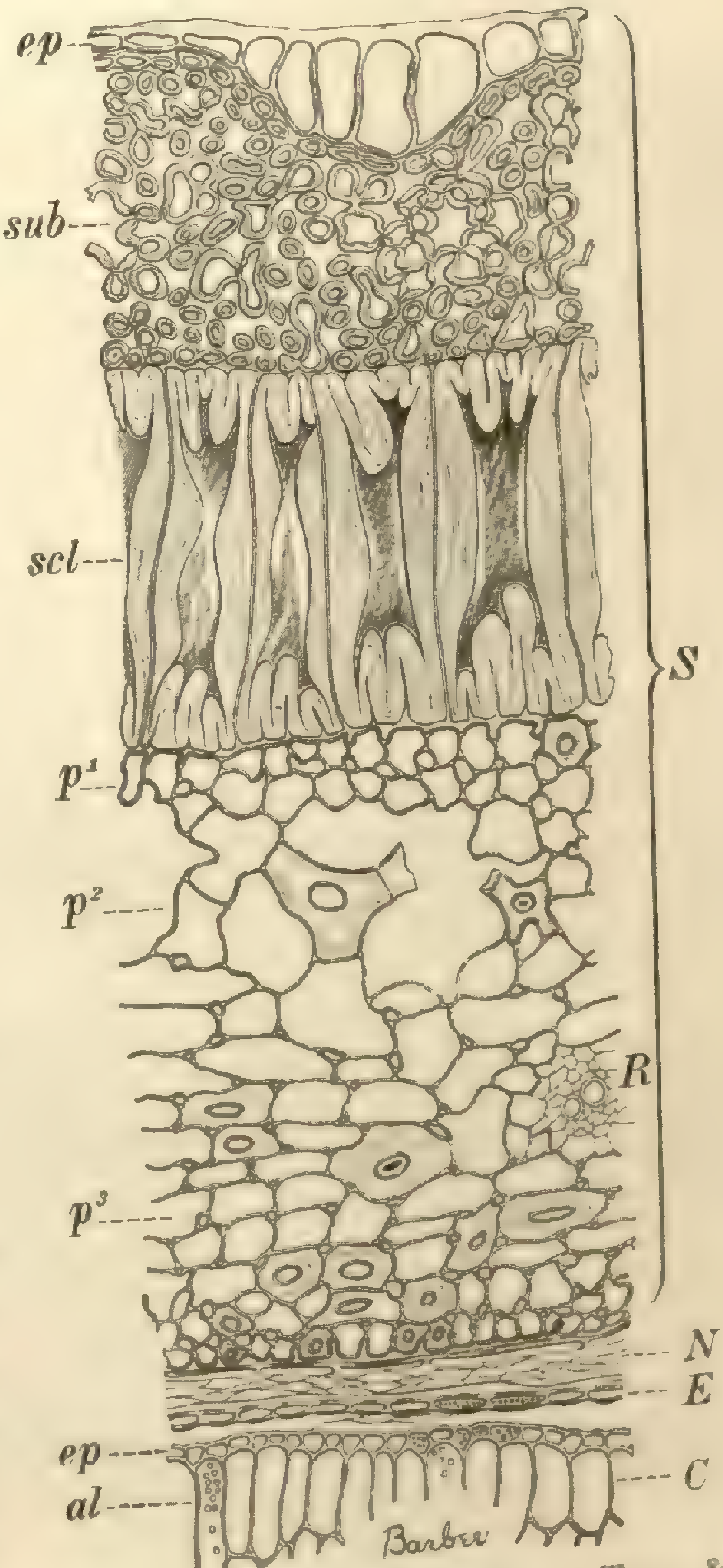


FIG. 40.—*Echinocystis lobata* Torr. & Gr. Seed in cross-section; *S*, spermoderm consisting of *ep*, epidermis, *sub*, subepidermal layer, *scl*, sclerenchyma, p^1, small-celled sclerenchymatized parenchyma, p^2, spongy sclerenchymatized parenchyma with *R*, raphe bundle, p^3, spongy parenchyma; *N*, perisperm; *E*, endosperm; *C*, cotyledon with *ep*, epidermis, and mesophyll containing *al*, aleurone grains. ×160.

5. *Inner mesocarp.*—Groups of small parenchyma cells, with structure similar to that of the middle mesocarp, are found between the bundles.

The numerous large bundles make up the bulk of the mature mesocarp, the anastomosing branches forming the fibrous network. Into each of the spines passes a small bundle which connects with this netted system.

Latex tubes are present in the young fruit, but very few or none are found with the dry bundles of the mature pericarp.

6. The *endocarp* (*fig. 41*) persists on the seed as a single layer of very thin-walled cells, longitudinally elongated and arranged side by side in groups.

SPERMODERM (*figs. 40, 42, 43*).—This thick, hard coat is best studied after bleaching with Javelle water.

1. *Epidermis* (*ep*).—The cells differ markedly from those of the seeds previously described in that they vary greatly in height throughout, owing to irregularities, not in the sur-

face of the seed, but in the subepidermal layer. A cross-section best illustrates this characteristic feature. The cells are much shorter than broad, except where they suddenly elongate, running down into the grooves of the subepidermal layer to form palisade cells about 54 μ in height. In surface view the whole radial wall is thickened, without the thickened rods so characteristic of other seeds.

2. *Subepidermal layer* (*sub*).—This coat, which varies in thickness as above described, always consists of numerous (ten to fifteen) layers of sclerenchymatized cells. They are very loosely arranged, with large circular spaces surrounded by thickened walls. In cross-section the tissue appears only as a confused mass of cells, but in tangential section (*fig. 42*) the contour of the walls is very distinct. The seed owes its color to the dark contents of the outer cell layers.

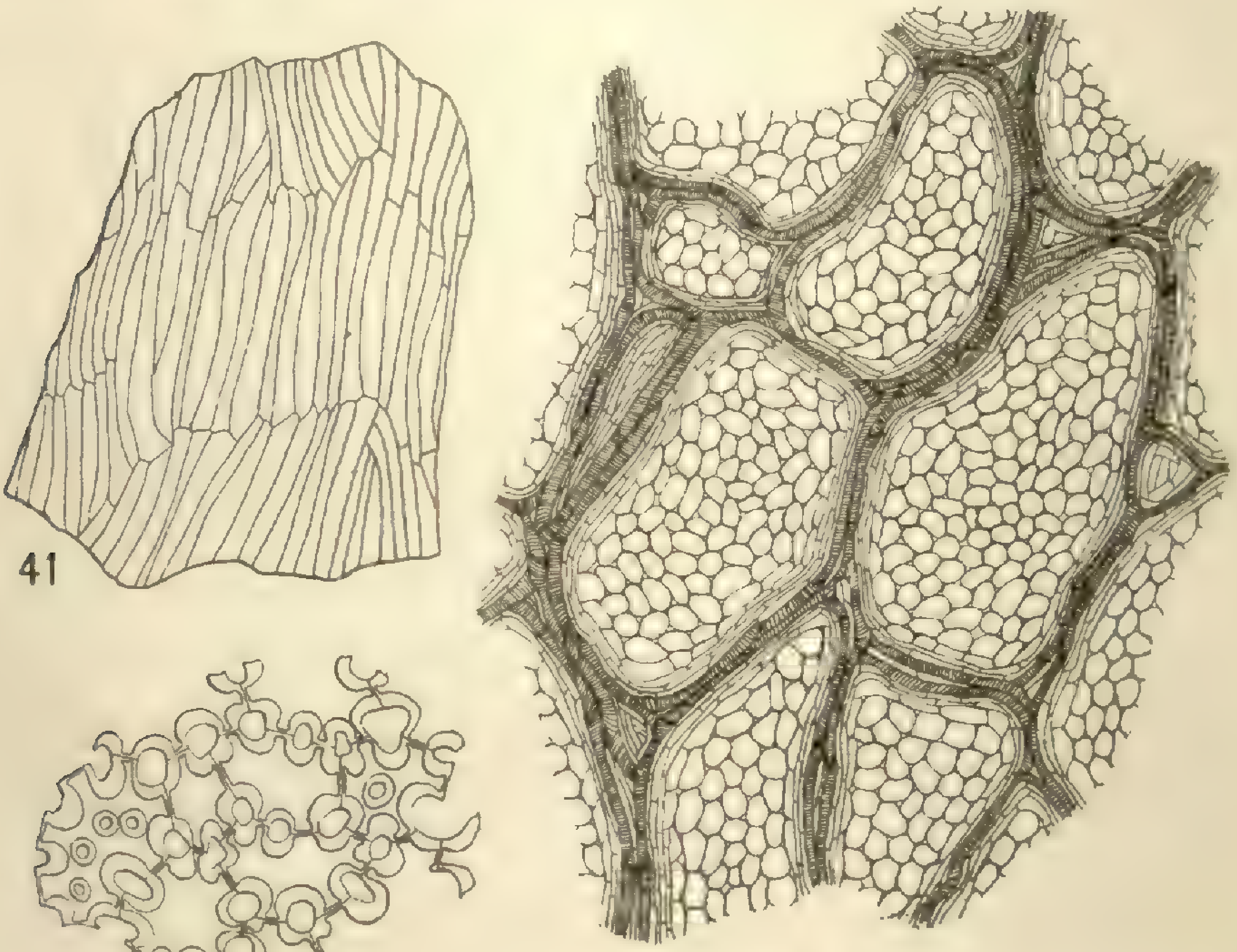


FIG. 41. *Echinocystis lobata* Torr. & Gr. Endocarp in surface view. ×300.—FIG. 42. *Echinocystis lobata* Torr. & Gr. Subepidermal layer in tangential section. ×300.—FIG. 43. *Echinocystis lobata* Torr. & Gr. Parenchyma with raphe in surface view. ×80.

3. *Sclerenchyma* (*scl*).—In cross-section this single cell layer appears as a palisade tissue, the cells, while only 40 μ broad, being radially elongated to 180 μ. The walls are extremely thick and the

cavities narrow, each sending out branches to the layers above and below. The folds of the sinuous outer and inner walls are also conspicuous in cross-section. In surface view the cells have sinuous walls and are irregularly arranged.

4. *Parenchyma.*—The outer layer (p^1) consists of small, thin-walled, and sclerenchymatized cells without pits. It bears no resemblance to the corresponding layers of Cucurbita. Adjoining this layer are two or three layers of true spongy parenchyma with large cells, thin walls, and large intercellular spaces (p^2). From this tissue the cells decrease in size inward for about fifteen layers (p^3).

The branching and anastomosing *raphe* ramifies through this inner parenchyma. Although each branch contains but few bundle elements, the branches are so numerous that they form a conspicuous tissue, best seen in surface view (*fig. 43*).

5. The *inner epidermis* corresponds in structure to that of *Cucurbita Pepo*, consisting of a layer of small cells with thin walls, the circular contour of the radial walls being very noticeable.

Perisperm (*fig. 40, N*).—The structure of this tissue is the same as that of the seeds already described, consisting of several layers of thin-walled parenchyma and an outer epidermis with cuticularized outer and radial walls. The epidermal cells are elongated, in many places transversely.

Endosperm (*fig. 40, E*).—One layer of uniformly thickened cells, containing protein granules, forms this coat. In one or two seeds examined there were indications of broken-down parenchyma.

The embryo (*fig. 40, C*) corresponds to the general description, the cotyledons having minute epidermal cells and mesophyll filled with oil and protein granules.

LUFFA CYLINDRICA ROEM.

The smooth, flattened seed (*fig. 44*) is 12^{mm} long, $6–7^{mm}$ broad, and $2–3^{mm}$ thick, of a dark-brown or black color.

Spermoderm (*figs. 45–47*).—This is thick and consists of the following layers:

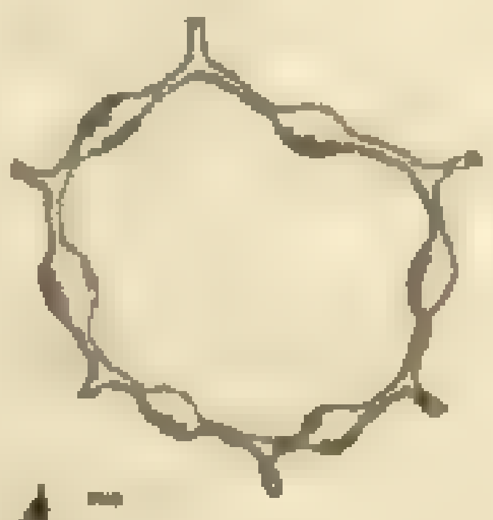
1. *Epidermis* (*ep*).—The palisade layer varies from $30–60\,\mu$ in thickness, the outer surface having a sinuous contour. On each of the radial walls is a single rod (*fig. 45*) which, instead of ending free

at the outer end, joins the thickened outer wall. The contents are of a dark-brown color.

2. The *subepidermal layer* (*sub*) consists of two quite distinct tissues. Within the epidermis is a layer, one to five cells thick, consisting of small reticulated or pitted cells. In tangential section (*fig. 46*) the zig-zag walls are seen to project into the cavity, with an intercellular space in the angle of each projection.

The second tissue consists of one layer of cells, 20 μ in thickness, polygonal and regularly arranged in cross-section, and slightly elongated tangentially.

3. A *sclerenchyma layer* (*scl*) of cells radially elongated up to 235 μ forms this characteristic layer. The outer and inner walls are sinuous, sending out peculiar branches. The cavity, best seen in cross-sec-



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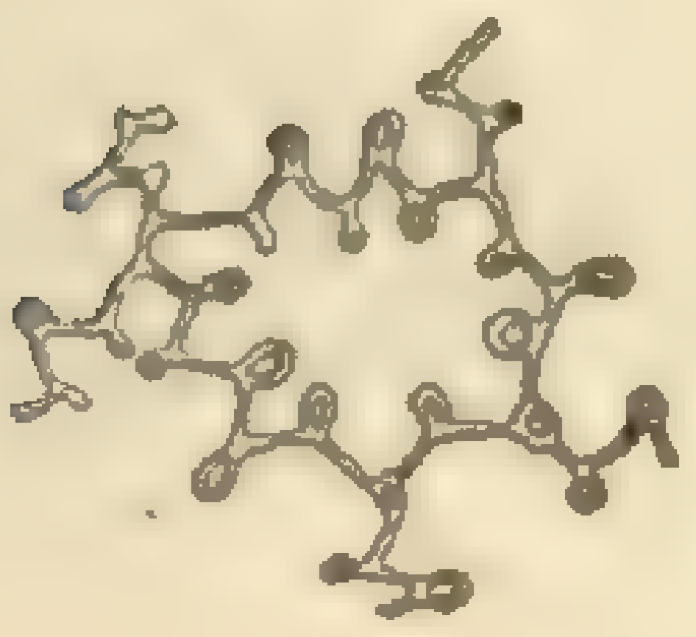

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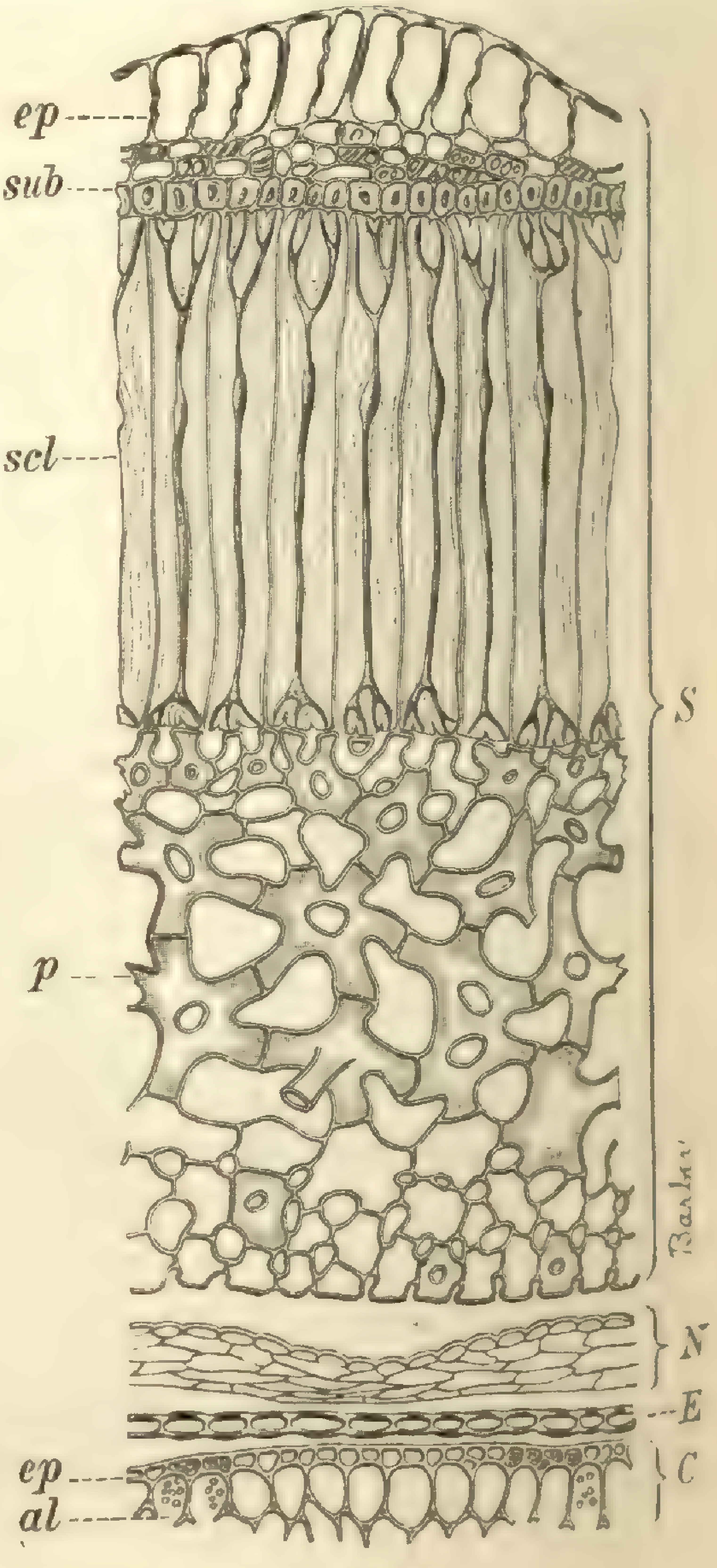

47

Fig. 44. *Luffa cylindrica* Roem. Seed. ×1.—Fig. 45.—*Luffa cylindrica* Roem. Tangential section of spermoderm, showing rods on radial walls of epidermis. ×160.—Fig. 46. *Luffa cylindrica* Roem. Tangential section of spermoderm, showing radial walls of subepidermal layer. ×300.—Fig. 47. *Luffa cylindrica* Roem. Seed in cross-section; *S*, spermoderm consisting of *ep*, epidermis, *sub*, subepidermal layer, *scl*, palisade sclerehncyma, *p*, parenchyma; *N*, perisperm; *E*, endosperm; *C*, cotyledon with *ep*, epidermis, and mesophyll containing *al*, aleurone grains. ×160.

tion, is extremely narrow, with a globular enlargement just without the center, the two ends branching and running into pits at the outer and inner tangential walls. In tangential section the polygonal cells are 30–45 μ in diameter.

4. *Parenchyma* (*p*).—A number of layers of large stellate cells form the spongy parenchyma. All the walls are thin, the cross walls being pierced with pits. In the outer layers the walls are sclerenchymatized.

5. *Inner epidermis.*—This layer of small parenchyma cells is also somewhat stellate.

The PERISPERM (*fig. 47, N*), ENDOSPERM (*fig. 47, E*), and EMBRYO (*fig. 47, C*) are of the usual type.

ABOBRA VIRIDIFLORA COGN.

The seed of *Abobra viridiflora* Cogn. (*fig. 48*) is 7–8^{mm} long, very slightly flattened, the enlarged apex being 2–3^{mm} broad and 1.5–2^{mm} thick, of a deep-brown color with longitudinal dashes of a darker brown.

SPERMODERM (*fig. 49*).—Thin but firm.

1. *Epidermis* (*ep*).—The palisade epidermis varies in thickness from 16–45 μ. On the thick radial walls of the larger cells are one or more straight rods joining the outer wall, which is extremely thick.

2. *Subepidermal layer* (*sub*).—This broad layer, six to ten cells thick, consists of very thick-walled, pitted cells irregularly arranged. The outer, and frequently the inner, cells are small, but the middle ones are of enormous size. Few or no intercellular spaces are present.

48

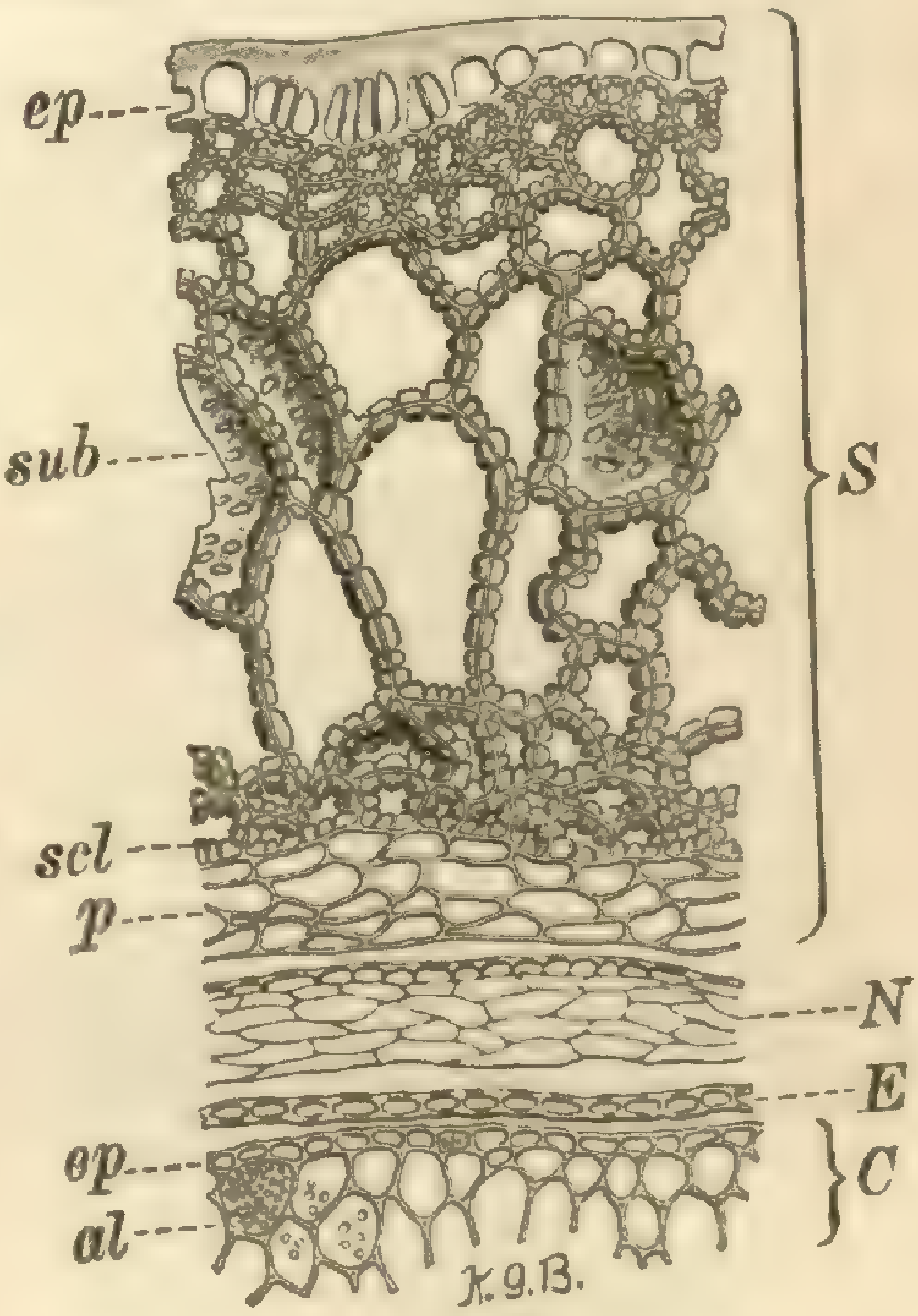

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FIG. 48. *Abobra viridiflora* Cogn. Seed. ×1.—FIG. 49. *Abobra viridiflora* Cogn. Seed in cross-section; *S*, spermoderm consisting of *ep*, epidermis, *sub*, subepidermal layer, *scl*, sclerenchyma, *p*, parenchyma; *N*, perisperm; *E*, endosperm; *C*, cotyledon with *ep*, epidermis, and mesophyll containing *al*, aleurone grains. ×160.

3. *Sclerenchyma* (*scl*).—Small, thick-walled, pitted, irregularly arranged cells make up this layer, which has no sharp line of demarkation from the preceding layer.

4. The *parenchyma* (*p*) consists of several layers of small thin-walled cells.

5. *Inner epidermis*.—One layer of parenchyma cells makes up this indistinct inner tissue.

The PERISPERM (*fig. 49, N*) of several cell layers, ENDOSPERM (*fig. 49, E*) of one layer of thick-walled cells, and EMBRYO (*fig. 49, C*) are like those described in the introduction.

MELOTHRIA SCABRA COGN.

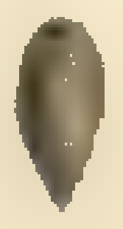


FIG. 50.—*Melothria scabra* Cogn. Seed. × 1.

The yellow-white seed (*fig. 50*) is 4–5^{mm} long, 2^{mm} broad, and 0.75^{mm} thick, flattened, pointed, and smooth.

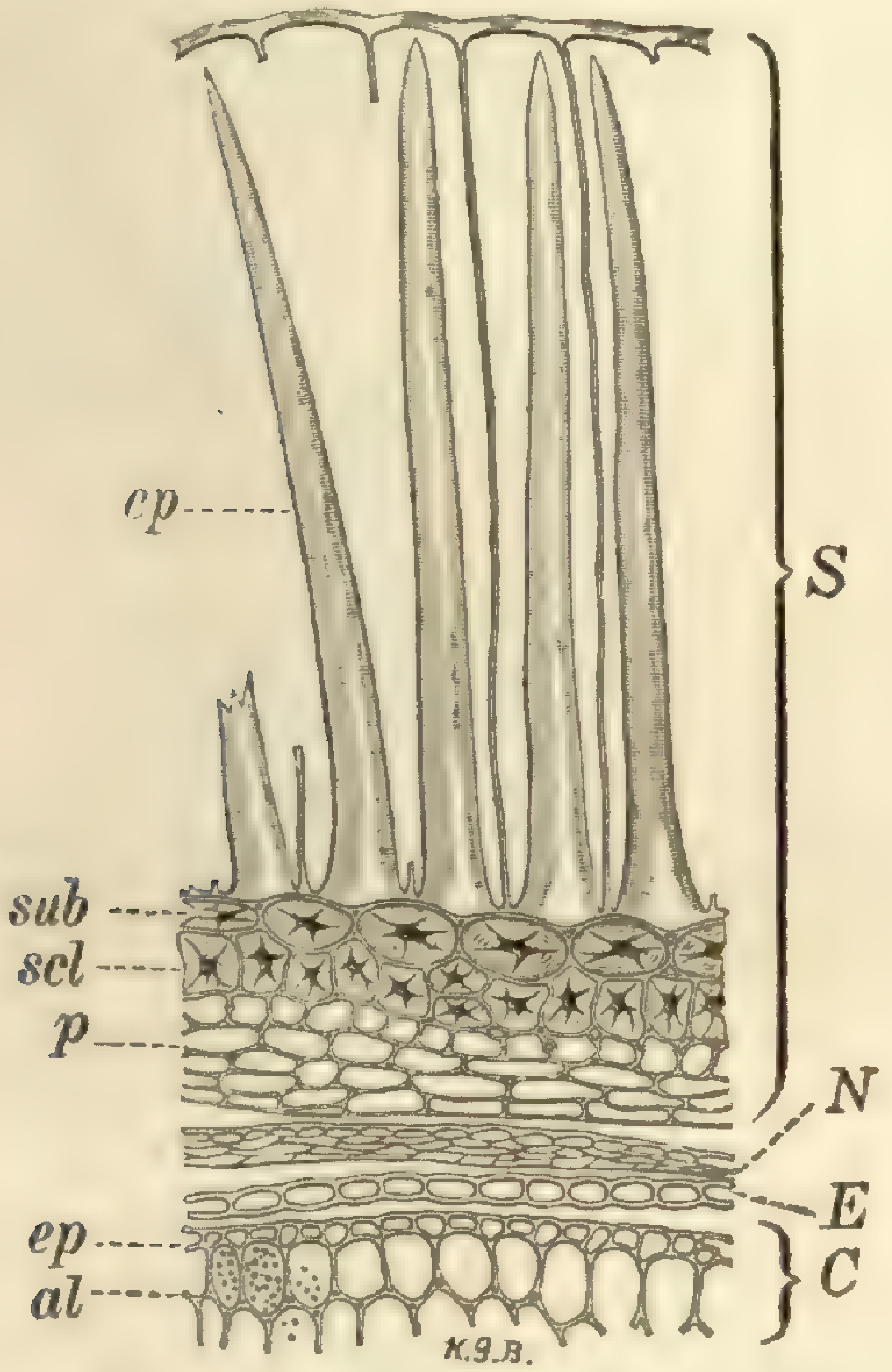


FIG. 51.—*Melothria scabra* Cogn. Seed in cross-section; *S*, spermoderm consisting of *ep*, epidermis, *sub*, subepidermal layer, *scl*, sclerenchyma, *p*, parenchyma; *N*, perisperm; *E*, endosperm; *C*, cotyledon with *ep*, epidermis, and mesophyll containing *al*, aleurone grains. × 160.

SPERMODERM (*fig. 51*).—Consists of five layers, and has a microscopic structure resembling that of *Cucumis sativus*.

1. *Epidermis* (*ep*).—A palisade layer, 270 μ in width, forms the outer layer, which, as in Cucumis, is frequently absent on the dry seeds. The walls are thin except for a single, straight, pointed rod on each radial wall.

2. *Subepidermal layer* (*sub*).—This single layer is composed of thick-walled cells having pits and distinct laminations. At the edge of the seed the layer increases from two to five cells in thickness, the outer ones being elongated radially.

3. *Sclerenchyma* (*scl*).—Small pitted cells, longitudinally elongated, make up the third layer.

4. *Parenchyma* (*p*).—Several layers of thin-walled parenchyma without characteristic features form the inner tissue of the spermoderm. Only with high magnification can the pits in the outer layer be seen.

5. *Inner epidermis.*—As in the other species, this tissue consists of a single layer of thin-walled cells.

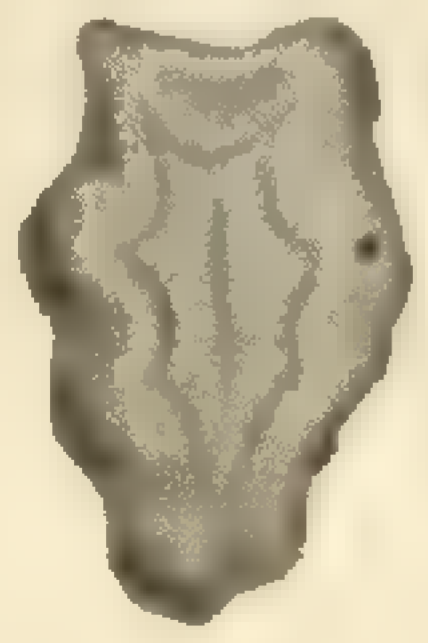
The PERISPERM (*fig.* 51, *N*), ENDOSPERM (*fig.* 51, *E*), and EMBRYO (*fig.* 51, *C*) correspond with the general description.

TRICHOSANTHES COLUBRINA L.

The seeds are 15^{mm} long, 8–9^{mm} broad, and 4–5^{mm} thick, of a gray-brown color. The irregular contour and beautiful dark markings on the flattened surface are illustrated by *fig.* 52.

SPERMODERM (*fig.* 53).—A very hard and thick seed coat with two distinct subepidermal layers is characteristic of this seed.

1. *Epidermis* (*ep*).—This layer is very irregular in width (12–135 μ). The larger cells, running down into grooves of the second layer, bear straight rods on their radial walls. These rods join the thickened outer wall and in cross-section are indistinguishable from the walls at the angles. All of the walls are impregnated with a



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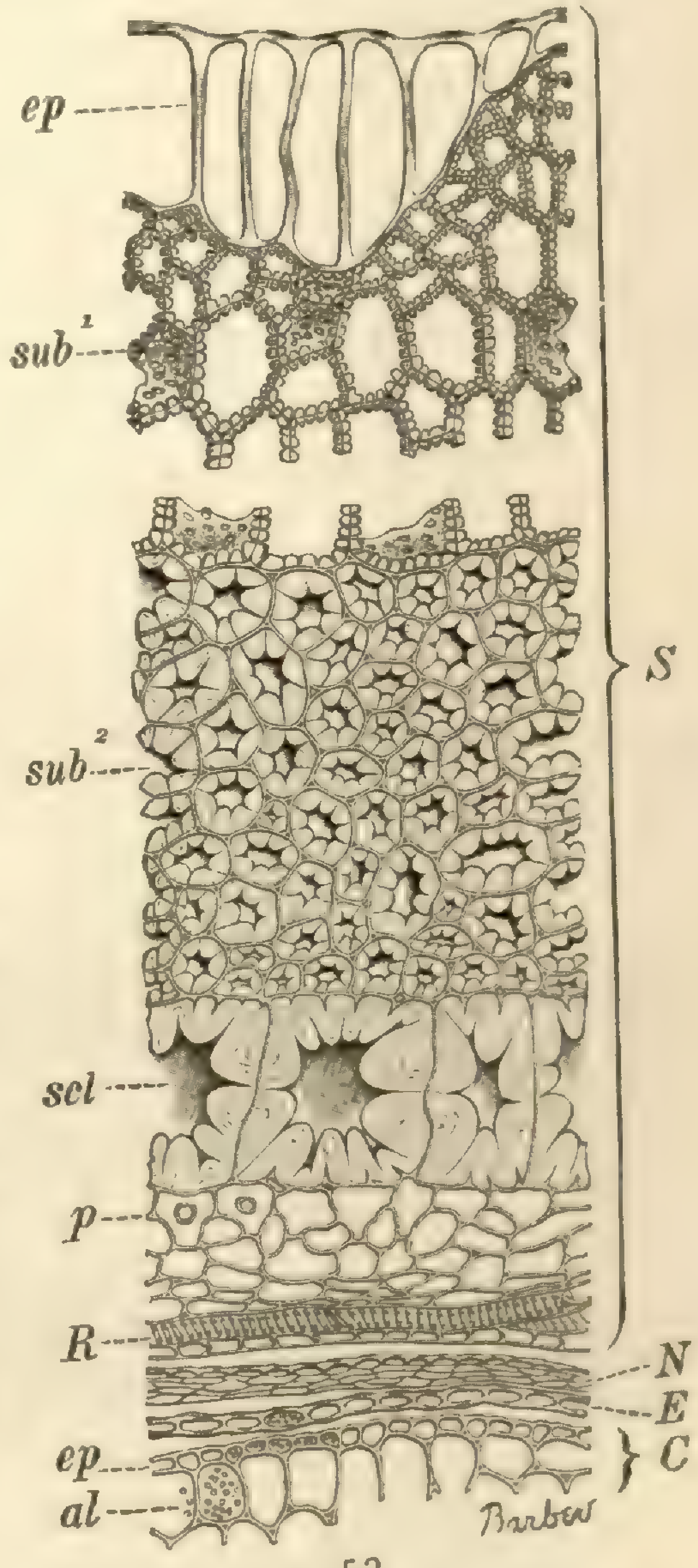

53

FIG. 52. *Trichosanthes colubrina* L. Seed. ×1.—FIG. 53. *Trichosanthes colubrina* L. Seed in cross-section; *S*, spermoderm consisting of *ep*, epidermis, *sub*¹, outer and *sub*², inner subepidermal layers, *scl*, sclerenchyma, *p*, parenchyma with *R*, raphe; *N*, perisperm; *E*, endosperm; *C*, cotyledon with *ep*, epidermis, and mesophyll containing *al*, aleurone grains. ×160.

brown coloring matter and starch is present in considerable quantity.

2. *Subepidermal layer.*—As previously stated, this layer is divided into two distinct tissues: the outer (*sub*[1]) consists of cell layers increasing in size from the small outer cells inward, with numerous pits in the thickened walls; below this tissue is a second (*sub*[2]), many cells thick, consisting of very thick-walled cells with small branching cavities and small intercellular spaces at the angles. The walls of both tissues are brown.

3. The *sclerenchyma* (*scl*), consisting of large, longitudinally elongated cells of the general type, forms a third sclerenchyma tissue which is impregnated with a brown substance.

4. *Parenchyma* (*p*).—Medium-sized thin-walled cells, the outer layer somewhat stellate, make up this layer. Chlorophyll is present in the inner layers in considerable quantity.

The *raphe* (*R*) branches out over the sides of the seed, the small bundles being found throughout the inner parenchyma.

5. An *inner epidermis* of thin-walled parenchyma cells completes the spermoderm.

The cells of the PERISPERM (*fig. 53, N*), ENDOSPERM (*fig. 53, E*), and EMBRYO (*fig. 53, C*) are not characteristic in this species.

YALE UNIVERSITY

THE ANATOMY OF ISOETES

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 126

ALMA G. STOKEY

(WITH PLATES XIX—XXI)

There is no group of plants among pteridophytes whose anatomy has occasioned so much discussion as the genus Isoetes. The most recent writers, FARMER on *I. lacustris*, R. WILSON SMITH on *I. echinospora*, and SCOTT and HILL on *I. Hystrix*, disagree in many points. In view of the lack of harmony, both of observation and interpretation, it has seemed advisable to make a comparative investigation of the anatomy of several American species.

Historical

The literature on the anatomy of Isoetes began in 1840 with a paper by VON MOHL (**24**). Although he recognized the lycopod affinities of Isoetes, he noted several important points of difference, in the arrangement and structure of the roots, and in the nature of the cambium products. Ever since that day the question of the nature of the cambium activity has afforded a fertile field for discussion, and it is with that subject that this paper is chiefly concerned. VON MOHL regarded the whole of the secondary growth as parenchymatous, and states that, as in other vascular cryptogams, there is no increase in thickness of the wood. The next significant work was that of HOFMEISTER (**16**) in 1857. In discussing the cambium products he says (p. 361): “The effect of the yearly renovation of the cambial layer is not only to increase and renew the cortical tissue, but new spiral cells also become added, although only sparingly, to the wood of old vigorous plants. Individual cells of the cambium, separated by two or three cambium cells from the older principal mass of the wood, often exhibit thickenings of the walls, which by their delicacy and want of color betray their undoubted recent origin.” In 1873 appeared RUSSOW'S *Vergleichende Untersuchungen der Leitbündel-Kryptogamen* (**18**), with a discussion of the anatomy of *I. lacustris*, *I. echinospora*, and *I. Hystrix*. This paper has had great influence on subsequent work, and to RUSSOW'S work may be attributed the current conceptions of the nature of the cambium products, i. e., that the cambium produces cortex externally to itself, but internally it produces a tissue which he calls the "prismatic layer," and this he regards as being made up of phloem cells, tracheids, and parenchyma. HEGELMAIER (**12**), writing in 1874, is inclined to question RUSSOW's interpretation, but adds that no decisive grounds can be given against the interpretation of the *Dauerzellen* as soft bast. FARMER (**9**) published in 1890 a very full discussion of *I. lacustris.* He seems reluctant to accept RUSSOW'S theory of the nature of the cambium products, but does not offer another. After quoting RUSSOW he adds: "Quite apart from the fact that it is produced internally to the cambium and would, from the point of view of its position, be anomalous, its structure is remarkably complex and heterogeneous." In discussing the structure of the "prismatic layer" he says:

> The zone-like arrangement consists in alternations of tubular thin-walled cell-rows of varying thickness, whose cell contents are clear and watery, with others, whose cells are wider in the radial direction, and filled densely with starch. Occupying a middle position in the latter zone is embedded an irregular ring of cells whose walls are thickened like those of the tracheids, but these too, unlike the latter, often contain protoplasm and starch.

In 1900 R. WILSON SMITH (**22**) discussed the morphology of *I. echinospora*, with some incidental work on its anatomy. His observations do not agree with those of FARMER on *I. lacustris*, and he proposes "to drop the term phloem until its justification is established on physiological grounds." In the same year there appeared a very exhaustive paper on *I. Hystrix* by SCOTT and HILL (**19**). The nature of the cambium products was taken up, and RUSSOW'S conception was indorsed, in that they regard the secondary tissues internal to the cambium as consisting of secondary tracheids, parenchyma, and phloem. Their statement is as follows:

> The cambium in *I. Hystrix*, arising in the tissues just outside of the xylem cylinder, continues its activity indefinitely, producing parenchyma, phloem, and a variable amount of secondary xylem on its inner side, and secondary cortical parenchyma only, towards the exterior.

Each of the last three writers has based his conclusion on the study of a single species, while RUSSOW, who investigated three forms, was hampered by the fact that he worked on herbarium material. The desirability of a comparative study of several species embracing a considerable range of habit is obvious.

Material

I am indebted for material of *I. Tuckermani* var. *Harveyi* (A. A. Eaton) Clute (*I. Harveyi* A. A. Eaton) to Dr. LEROY H. HARVEY, who made a collection at Pushaw Pond, Maine, of plants in various stages of development; to Mr. WILHELM SUKSDORF for material of *I. Nuttallii* Engelm. (*I. Suksdorfii* Baker) collected at Bingen, Wash.; and to Dr. H. C. COWLES for material of *I. echinospora* var. *Flettii* which he collected at Spanaway Lake, Wash., in the summer of 1907. The latter material has been kept in cultivation at the greenhouses of the University of Chicago and has afforded abundant material for the study of a close series of stages in the development of the stem. I am also indebted to the late Mr. A. A. EATON of the Ames Botanical Laboratory, North Easton, Mass., for the determination of *I. melanopoda* Gay.

For killing and fixing the stems a medium solution of chrom-acetic acid was used. The material was embedded in paraffin and cut in serial sections 7 to 12 μ thick. Some of the series were transverse and others longitudinal, both parallel and perpendicular to the furrow. A considerable number of stains and combinations of stains were used, of which the most satisfactory were the following: a combination of safranin and anilin blue devised by Dr. LAND; iodin green and Bismarck brown; iodin green and eosin.

The four species studied present a considerable range in habit. *I. Tuckermani* var. *Harveyi* is a submersed form which grows in water 30–150$^{\mathrm{cm}}$ deep. The trunk is deeply two-lobed, occasionally three-lobed. The leaves are short, strongly recurved, without stomata, and said by Eaton (**8**) to be relatively the stoutest of any North American species, being 5–6$^{\mathrm{cm}}$ in length and 2.5–3$^{\mathrm{mm}}$ in diameter. *Isoetes echinospora* var. *Flettii* grows on the gravelly edges of mountain lakes in Washington. In the spring it may be submersed, but during most of the year it is out of the water. The gravel holds water so that the substratum is never very dry. The trunk is two-lobed and the leaves are moderately stout. The largest form studied is *I. melanopoda*. It has a large two-lobed trunk, with very long, moderately stout leaves. It grows in inundated fields and shallow ponds, where it is emersed during most of the summer. *I. Nuttallii* has a three-lobed trunk and long, very slender leaves. It never grows under water, but near springs or springy places, and on low wet grounds or meadows, where the ground becomes very dry in the latter part of the season.

Investigation

The complicated structure and arrangement of the old stem is more easily understood by a study of the sporelings. The stem of a sporeling is a mass of undifferentiated parenchyma, traversed by leaf traces, which come together to form the short flat stem plate and continue outward and downward into the roots. All observers agree that in the young plants there is no cauline portion in the stem bundle, but whether or not there is a cauline portion in the older stems has long been a disputed point. HOFMEISTER, DE BARY, CAMPBELL, and FARMER look upon the stem bundle as being made up of leaf traces; while HEGELMAIER, BRUCHMANN, and SCOTT and HILL maintain that there is a cauline portion. In the short and compact stem there are no indications of a procambial strand, and as there are never any tracheids present above the last leaf trace, the evidences of a cauline portion are not satisfactory. In following the cross-sections of leaf traces in a series of longitudinal sections up to the place where the traces coalesce, it is easily seen that there is a sufficient amount of tracheary tissue in the leaf traces to account for all the xylem in the stem bundle. SCOTT raised the objection that the tracheids of the stem are unlike those of the leaves, but there is no greater difference between the tracheids of the stem and of the base of the leaf, than between those of the base of the leaf and of the upper part. The difference is chiefly one of length, and this, together with differences in the distribution of the thickening of the walls is correlated with the rate of growth of the part in which the tracheids are found.

In all plants there is a separation into root and stem regions, and this becomes more marked as the plant enlarges. This suggests that the tuberous body is not wholly stem, but a contracted stem and main root. Owing to the compact growth and the consequent displacement of tissues, some of the root bundles in an old plant may be found higher up in the cortex than the old leaf traces. In fact it is not uncommon, in sections of old stems cut at the very apex of the stem, to find in the cortex a longitudinal section of a root making its way out. Hence, although the stem and root regions are sharply marked off in the central axis, it is impossible to delimit these regions in the cortex. In the young plant shown in *fig. 4*, all the leaf traces and root bundles are functional. In the plants shown in *figs. 19, 20*, all the roots are dead except a few at the bottom, and all the leaf traces except a very few at the top. As the plant increases in size, the old leaf traces are unable to keep up with the growth of the stem and are torn apart, leaving the old stumps attached to the central axis, while the rest of the leaf trace is carried out farther and farther by the growth of the cortex, and in time is sloughed off.

The arrangement of the roots is described in great detail by SCOTT and HILL for *I. Hystrix*, a three-lobed form. The two-lobed trunks show no essential variation from that type, and it is therefore not necessary to give a detailed discussion of the subject. *Fig. 6* illustrates the appearance of the lower part of the stem in cross-section, showing the relative position of the roots of various ages. The roots near the center, which are outlined by dots, are those in meristematic condition; next to them are the mature active roots which are indicated by shaded circles; beyond the mature roots are those which are dead and crushed. The relation of the sets of roots is indicated in *fig. 19* also. The arrangement of the roots in the two-lobed species was first correctly worked out by HOFMEISTER; the youngest sets of roots are those nearest the furrow; and of those in the furrow, the youngest are at the ends.

THE ROOT

The structure of the roots has been described so many times that it is unnecessary to take it up in detail. The most interesting feature is that they are collateral and monarch, without showing any traces of reduction. As the root bundle passes out from the vascular axis it is a round or flattened bundle surrounded by parenchyma. At a short distance from the stem, phloem replaces the parenchyma on the side away from the center of the stem. The phloem is always limited to one side and is small in amount in comparison with the xylem. There is also proportionally much less than in the leaf traces. The protophloem and protoxylem are usually differentiated about the same time, but the protophloem occasionally precedes the protoxylem. The complete differentiation of the phloem is usually complete before that of the xylem. The differentiation of the xylem in the roots is much slower than in the leaf traces. *Fig. 7* illustrates the structure of a root bundle before it is completely developed and while it is still in the cortex. The eccentric position of the bundle in mature roots is shown in *fig. 8*. While the root bundle is making its way through the cortex the endodermis is poorly differentiated, but in the mature root outside of the stem it is well defined. The pericycle is poorly developed. It is usually entirely absent opposite the phloem, but opposite the xylem there is usually a small amount.

THE LEAF

The leaves of the four species studied present considerable variation, both in general appearance and anatomy.

The leaf of *I. echinospora* var. *Flettii* is moderately stout, and quadrangular in outline (*fig. 9*). In the cortex and lower part of the leaf the bundle is fairly well developed, but above the sporangium it becomes a slender strand. The bundle is collateral throughout, but tends to become concentric in the upper part. The differentiation of the phloem regularly precedes that of the xylem, as was found by KRUCH (**17**) in the species which he studied. The protoxylem in most cases is plainly exarch, but sometimes the differentiation is nearly simultaneous. In this species I found no cases of distinctly mesarch protoxylem. It is common for the metaxylem to develop in three directions from the protoxylem, but I found no cases in which it developed on the fourth side, i. e., on the side toward the phloem, although KRUCH and SCOTT and HILL find that in their species the bundle tends to become mesarch in the region of the sporangium. There is evidently a certain difference in this respect in different species, for in *I. Nuttallii*, which I shall discuss later, mesarch protoxylem is sometimes present. While the protoxylem and metaxylem are both composed of spiral and annular tracheids, or tracheids with irregular spirals, the protoxylem can usually be recognized by the fact that the spirals and rings are looser. The protoxylem cells of the lower part of the leaf are small and are the first to show signs of crushing, but those in the upper part are large and later form canals by the loss of the thickened portions. In the upper part of the leaf the protoxylem is usually limited to a single large vessel, whose place can be recognized in old leaves by the large canal formed by its disappearance (*fig. 13*); but in the lower part of the leaf, as well as in the leaf trace, the protoxylem cells are smaller, several in number, and less sharply marked off from the metaxylem. *Fig. 10* represents the section of a young leaf near the tip, in which the only indication of the protoxylem is the large central cell, which is not yet thickened, while the phloem is represented by several cells. The phloem consists of very long and slender tubes whose sieve plates are terminal. They come out clearly in sections stained in anilin blue or Bismarck brown. Although several preparations suggest the presence of thin areas on the lateral walls, the evidence is not conclusive. In the portion of the leaf above the ligule there is a very abrupt decrease in the amount of xylem, but not a corresponding decrease in the phloem. The phloem is well developed throughout, but instead of forming a band on one side of the bundle, as in the lower part of the leaf, it forms an arc. The phloem does not disappear from the center of the arc, leaving two lateral groups such as KRUCH has described in *I. Hystrix*, *I. Duriaei*, and *I. velata*, but the amount in the center of the arc is variable. Near the top of the leaf the phloem is sometimes most abundant in the middle of the arc. In *fig. 14* is shown a leaf trace from the cortex at the base of the leaf. This is the type of bundle which is found in the leaf trace as it traverses the outer part of the cortex, and in the leaf itself from its base to the ligule. Just above the ligule, the bundle passes abruptly into the reduced type of *fig. 13*. In the former, the tracheids, which are fairly uniform in size, are scattered among parenchyma cells that have abundant protoplasm and large nuclei. Before the sporangium is mature, the outer vessels, the protoxylem, begin to collapse. In this type of bundle the phloem is always in a band and shows no tendency to surround the xylem. The amount of phloem is less than in the upper part of the leaf, and by the time the leaf is mature it is almost entirely obliterated by crushing. In following the bundle through the cortex toward the center of the stem the first change seen is a condensation of the bundle by a reduction in the amount of parenchyma, although a few parenchyma cells usually remain in the center as long as the leaf trace can be identified (*fig. 15*). For some distance the compact bundle remains distinctly collateral, but the phloem decreases in amount, and near the stele disappears entirely, the leaf trace consisting of a strand of xylem with a few parenchyma cells in the center and a parenchyma sheath. The xylem cells become shorter, and it is no longer possible to distinguish between protoxylem and metaxylem. The next stage is the merging of the tracheids and parenchyma of the various leaf traces to form the central axis.

While in general the leaf traces of the other species are similar to those of *I. echinospora* var. *Flettii*, they present certain interesting variations. The leaf of *I. Tuckermani* var. *Harveyi* is also quadrangular, but is shorter and more rigid. The bundle, however, is not so well developed, either in amount or structure. The tissues are not well differentiated; the phloem in particular is much less sharply differentiated than in the other three species. The thickening of the walls is slight and sieve plates are not evident. The amount of xylem is noticeably less, but the phloem, although not abundant, is not so much reduced as the xylem. In the lower part of the leaf the phloem is a narrow band, but in the upper part of the leaf it forms an arc and tends to surround the xylem. The formation of sieve cells begins in the middle of the band, or arc, and extends around three sides of the xylem. The phloem in the center of the arc is small in amount and more rudimentary than that on either side, so that in places there are indications of a tendency to form two lateral groups. The sieve cells in the lateral groups are smaller, as well as more numerous, and they continue to function long after the first-formed cells have become crushed and functionless. In this species the sporangia are comparatively small.

I. melanopoda has very long, moderately stout leaves, with large sporangia. The leaves have a greater diameter than those of *I. Tuckermani* var. *Harveyi*, but they are very much longer and relatively less stout. The amount of xylem is greater, and the bundle is in general stronger than in the two preceding species. The leaf trace in the cortex of the stem contains on an average twice as many tracheids as that of *I. Tuckermani* var. *Harveyi*, while in the leaf trace above the sporangium there may be three to eight tracheids instead of one to four, as in *I. echinospora* var. *Flettii* or *I. Tuckermani* var. *Harveyi*. As in the other species, the phloem forms an arc in the upper part of the leaf. As the phloem is abundantly developed at the sides of the arc and poorly developed in the middle, there is a tendency for it to separate into two lateral groups.

The leaves of *I. Nuttallii* differ considerably from those of the other species, both in external appearance and structure. They are triangular in outline, long and very slender, indeed almost thread-like. The sporangia are extremely large, while the leaf tissue, in the sporangium region as well as above, is notably small in amount. The bundle, however, is well developed and larger than in any of the preceding species. It differs conspicuously from those of the other species in the large amount of xylem present in the bundle above the sporangium and in the upper part of the leaf. Although, as in the other species, the bundle becomes reduced above the sporangium, there are usually eight or ten tracheids and sometimes fifteen or sixteen present for a considerable distance above the sporangium. In the region above the sporangium, as in the other species, the protoxylem consists of large cells, which are later replaced by canals. The walls lining the canals are heavily lignified. There is no trace of an endodermis, such as SCOTT and HILL find in *I. Hystrix*. The protoxylem in this region is occasionally mesarch, a few tracheids of the metaxylem developing on the side toward the phloem, although the greater amount of metaxylem is always on the adaxial side of the leaf, where it frequently forms a narrow band. In the region of the sporangium the metaxylem is in the form of a crescent, with the heaviest development often at the ends of the horns. In such cases the bundle tends to become mesarch. The phloem also is well developed and abundant, the sieve tubes regularly separating above the ligule into stout strands. A transverse sieve plate is shown in *fig. 11*.

If the four species are arranged in a series according to the size and development of the leaf traces, the series is as follows: *I. Nuttallii*, *I. melanopoda*, *I. echinospora* var. *Flettii*, *I. Tuckermani* var. *Harveyi*. If the species are arranged according to habitat, from terrestrial to aquatic, the order would be the same, with *I. Nuttallii* as the most terrestrial form and *I. Tuckermani* var. *Harveyi* as the most aquatic. A series arranged according to the size of the leaves is as follows: *I.*

melanopoda, I. Tuckermani var. *Harveyi, I. echinospora* var. *Flettii, I. Nuttallii.* A series according to the size of the sporangia is as follows: *I. Nuttallii, I. melanopoda, I. echinospora* var. *Flettii, I. Tuckermani* var. *Harveyi.* It is perhaps not safe to generalize from a comparison of only four species, but it is worthy of note that the size and development of the bundle in these forms is not related to the size of leaf, but follows the other two series, that of habitat and size of sporangium.

HILL (13) calls attention to the presence of two canals in the leaves of *I. Hystrix,* which he regards as representing the parichnos of the Lepidodendreae. In none of the four species examined is there any trace of a canal or any indication of a tendency to form canals. In this respect these species agree with *I. lacustris.*

THE STEM

As is well known, the stem of Isoetes is a short tuberous body, whose vascular axis is very small in proportion to the diameter of the stem. The stem grows in length very slowly, and the apical region is left in a deep pit by the overgrowth of the surrounding region. If the term stele may be applied to a region whose connection with a plerome is far from certain, then the vascular axis may be defined as a non-medullated monostele, consisting of xylem and parenchyma forming a loose network. The xylem is made up of short spiral, annular, and netted tracheids, whose long axis is transverse to the stem (*fig. 22*). The parenchyma cells contain abundant protoplasm, and the nuclei appear active. The xylem axis is surrounded by similar parenchyma cells, one to three layers deep, but in neither young nor old plants is there a trace of phloem. A great many young plants of *I. echinospora* and a few of *I. Tuckermani* var. *Harveyi* were examined, and in all cases the xylem is surrounded by undifferentiated parenchyma. In very young plants the vascular axis is exceedingly small, but there is a constant increase both in length and diameter with the increase in the number of leaves.

The differentiation into protoxylem and metaxylem, which is usually well marked in pteridophytes, is lacking in Isoetes. There is neither a difference in the time of development nor in the character of the elements. A difference in character of elements is not likely to occur in such a slow-growing stem, and a difference in time would be difficult to detect in a stele whose elements run transversely.

Scott and Hill have claimed a slight differentiation in time in certain cases, giving as evidence sections which show tracheids at the outside and parenchyma in the center. But since the xylem is made up of leaf traces which curve down from the leaves, as in *fig. 4*, it is evident that it would be possible to obtain a section which shows this condition without being an example of protoxylem differentiation. In young stems it is not uncommon to find that at least one section shows this apparent differentiation into protoxylem and metaxylem. As was mentioned above, an examination of a series of cross-sections of leaf traces as they approach the central axis indicates that there is no differentiation into protoxylem and metaxylem in that part of the leaf trace. Even if it were present in the leaf traces, the transverse arrangement of the tracheids would cause it to appear in tiers rather than in vertical strands, as in other pteridophyte stems.

The cambium, which appears very early (*fig. 3*), begins its activity in the parenchyma which surrounds the central axis, so that all the tissues which are found outside this thin layer of parenchyma are secondary. The secondary tissues of Isoetes have always been described as anomalous, and so have furnished a fertile field for observation and theorization. The cells which the cambium cuts off externally are ordinary thin-walled parenchyma cells, which have always been called cortex. Whether they represent ancestral phloem is, of course, an interesting question, but there is nothing in their structure to suggest an answer. This is the great storage region of the plant, and the amount of this tissue is much greater than that formed internally by the cambium. In the middle and outer regions of the cortex the cells become rounded, often lobed, as in the mesophyll of leaves (*fig. 18*), and always contain large amounts of starch. The cortex increases its thickness from year to year, although there is a continual loss by the sloughing-off of the outer layers. In the outer region there is little or no starch.

The tissue formed internally to the cambium, the so-called "prismatic layer," is that which has aroused the greatest interest. In a freshly cut section this layer is a glistening white and stands out sharply from the surrounding region. In stained sections it is seen that the "prismatic layer" is composed of several kinds of cells. In the four species studied there is a considerable range both in the types of cells and in their distribution.

In *I. echinospora* var. *Flettii* there is found scattered irregularly a rather large number of active nucleate parenchyma cells, whose walls are slightly thickened. Associated with them are other cells which are almost or entirely empty and whose walls are not uniformly thickened, but have round, oval, or irregular pits. In such cells the thickening is not very heavy. There are usually other cells in which the thickening is more pronounced and is arranged in irregular bands or rings. In some cells there are heavy bands in addition to the irregular pittings.

Of the four species, *I. Tuckermani* var. *Harveyi* most closely resembles the preceding species, but it differs in several points. There is little or no active parenchyma, the entire tissue consisting of cells whose walls are thickened irregularly. These cells are seldom entirely empty, but usually contain a little protoplasm and small, apparently degenerating, nuclei. The cells are for the most part of the type shown in *fig. 23*, in which the pits are small and irregularly distributed, and there are but faint indications of banding. In the older plants, however, it is not uncommon to find the thickening forming more or less definite bands. In the older parts of old plants the pits become smaller and less prominent, tending to disappear entirely. Sometimes the pits can be seen in sections stained in Bismarck brown, when with a less transparent stain, such as Delafield's hematoxylin, the pits cannot be distinguished, and the walls appear to have a uniform and rather heavy thickening. Apparently the thickening of the cell walls goes on through a period of several years, the first thickening being irregularly distributed, leaving irregular pits, while the later deposits include the whole of the wall and tend to obliterate the pits.

In *I. melanopoda* we have all the types of cells which have been described for *I. echinospora* var. *Flettii:* active parenchyma cells, pitted cells, and cells with irregular thickened bands or rings. The pitted and banded cells are as a rule entirely empty. In addition to these types of cells, however, there are other cells with banded thickenings which are slightly lignified, and also tracheids with spiral or annular thickenings, whose lignification is pronounced, although not as heavy as in the tracheids of the central axis or of the leaf traces (*fig. 21*). The parenchyma cells, however, have thinner walls and are richer in protoplasm than in the two species just described. The parenchyma and the various types of thickened cells are in most cases distributed irregularly, as is shown in *fig. 26*, although occasionally in the older parts of old stems there are indications of zonation.

I. Nuttallii shows the same type of cells as *I. melanopoda*, but there is a difference in arrangement. This species always shows the zonation which has been described by FARMER for *I. lacustris* and by HEGELMAIER for *I. velata* and *I. Duriaei*. The parenchyma cells form layers one or more cells thick, which alternate with layers composed of the various types of thickened cells (*fig. 25*). The zonation is evident in young plants and is very striking in old plants, especially in the older regions of the "prismatic layer." The thickened cells are usually entirely empty. The parenchyma cells of *I. Nuttallii* are larger, contain more protoplasm, and have thinner walls than those of the first two species. The parenchyma is more like that of *I. melanopoda*, although on the whole the cells are richer in protoplasm than those of the latter species. In the older parts of the stem the thickened empty cells are usually collapsed, so that the zones of thick-walled cells, which alternate with the well-developed parenchyma zones, are apparently much narrower.

Almost all the writers on Isoetes have called attention to the presence of the fine-grained starch in the cells of the "prismatic layer." This was first noted by HEGELMAIER in *I. velata* and *I. Duriaei*, in which the starch-containing parenchyma cells form zones alternating with zones of empty cells. FARMER records the presence of starch in the prismatic layer of *I. lacustris*, in which the starch-filled cells are also arranged in zones. The disposition of the starch was found to vary with the species. In *I. echinospora* var. *Flettii* and *I. melanopoda*, it is present abundantly in the cortex but not at all in the "prismatic layer." In *I. Tuckermani* var. *Harveyi*, in addition to the starch in the cortex, there is starch in the parenchyma in the vascular axis, and in the layer of parenchyma surrounding the axis, but there is none in the "prismatic layer." *I. Nuttallii* shows what seems to be the more common arrangement in the forms previously described; that is, there is abundant starch in the "prismatic layer."

It should be noted that the only one of the four species which contains starch in the "prismatic layer" is the only one which shows well-marked zonation, and is also the one in which the parenchyma cells are the largest and contain the most protoplasm.

Discussion of secondary thickening

A study of the structure of the cells composing the "prismatic layer" is of interest only as affording a basis for an interpretation of the nature of the layer. The interpretation which is accepted in the most comprehensive of all recent works on pteridophytes, BOWER'S *Origin of a land flora*, as well as in CAMPBELL'S *Mosses and ferns* and other current texts, is RUSSOW'S theory, which more recently has received the indorsement of SCOTT. As was mentioned above, they look upon the "prismatic layer" as a complex of tissues, consisting of parenchyma, phloem, and xylem. Among recent writers SMITH is the only one who has even suggested that the tissue may be of a less extraordinary nature.

The position of this layer would naturally lead to the conclusion that it is secondary xylem, but for the fact that its composition is not what we have been accustomed to look upon as characteristic of that tissue. The parenchyma is more abundant, while well-defined tracheids are not only few in number in most species but exceedingly rare or entirely absent in others. In addition to the parenchyma and tracheids, there are the pitted cells, which have been regarded as phloem. It may be well at this point to consider the evidence upon which this claim is made. SCOTT and HILL say:

> The phloem elements have an extremely characteristic structure of their cell walls which comes out conspicuously in sections stained in hematoxylin. Their walls are much pitted, the thicker bands of membranes between the pits forming a lattice-like reticulum. The pits are often subdivided by fine bars into smaller areas. Little of the nature of formed contents can usually be detected, but sometimes small, deeply staining globules are found adhering to the walls, and apparently localized at the pits. In the older parts of the stem the phloem is to a great extent obliterated, dense masses of callus-like substances appearing on the cell walls and almost filling the cavity. The masses stain like callus with coralline-soda, but the other callus reactions tried did not give wholly satisfactory results. We have not investigated the more minute histology of the phloem and thus have not demonstrated the perforations of the thin-walled areas. That may be left to other investigators, but in the meantime, we can scarcely doubt that these enucleate

elements, with the characteristic areolations of their walls, and their agreement in various reactions with the sieve tubes of the leaf, with which we shall see they are continuous, are best to be regarded as themselves representing the sieve tubes of the stem.

If no other explanation of these structures were possible, the reasons given above might be accepted as sufficient proof of the phloem nature of the pitted cells, although the fact of a cambium cutting off both phloem and xylem from the same face is so extraordinary that one does not expect the advocates of such a theory to content themselves with leaving the burden of proof to other investigators. The only analogy is in the case of Dracaena and its allies, whose anomalous secondary thickening has been frequently referred to in the literature on Isoetes. Before RUSSOW'S theory made its appearance, the tissue on the inside of the cambium had been regarded as secondary xylem. This was the very natural interpretation given by HOFMEISTER in his *Higher Cryptogamia* and was accepted, apparently without question, until RUSSOW'S more critical work appeared. If one is not willing to accept the RUSSOW theory, the natural alternative is to regard the "prismatic layer" as secondary xylem. This, of course, requires an explanation of its unusual structure. The presence of a large amount of parenchyma in the secondary wood is unusual but not without parallel, as this is the case in certain Lepidodendreae, e. g., *Lepidophloios fuliginosus*. The presence of unlignified pitted cells, of course, is the situation which has led to controversy, and is the chief point to be explained. However, the presence of pitted cells of a phloem-like aspect does not necessitate the assumption that the cells are phloem, since that structure is found in cells of other tissues, for example, the cortical parenchyma of *Helminthostachys zeylanica*. FARMER and FREEMAN (**10**) in their description of the pits in the cells of the cortical parenchyma say:

> The pits are remarkable, forming, as they do, not merely simple depressions in the walls, but rather being massed together in areas like the pores of a sieve plate. Indeed they may fairly be termed pitted areolae and they do not differ essentially from the actual sieve tubes themselves in the plant.

The presence of cells of this type in tissues which do not even belong to part of the bundle indicates that pitted walls are not necessarily to be taken as an indication of phloem. The usual phloem tests applied to the "prismatic layer" do not give any positive results. In the case of the cells in question it can be shown that not only are they not phloem but that they are xylem.

A careful examination of the "prismatic layer" of such forms as *I. Nuttallii* and *I. melanopoda* will reveal the fact that, while the secondary tracheids are far removed in appearance and staining reactions from the pitted cells, an almost perfect transition series exists between the two types. Several stages are shown in *fig. 21*. It is possible to trace a series from the tracheids with lignified spiral or annular thickenings, through those with less regular thickenings and with a smaller amount of lignin, to those in which the thickening is very irregular and which have no trace of lignin. A combination of safranin and anilin blue was found to be particularly valuable in revealing slight amounts of lignin. With this variation in wall thickening and lignification, there is correlated a variation in the amount of cell contents. The existence of the transitional stages leads almost inevitably to the conclusion that the various types of cells of the "prismatic layer" differ essentially only in their stage of development, and that the layer accordingly consists of mature tracheids, immature tracheids, and parenchyma. While the series in *I. echinospora* var. *Flettii* is less perfect, it is very suggestive, but that of *I. Tuckermani* var. *Harveyi* is usually too limited to afford much of an indication of the nature of the pitted cells.

The recognized steps in tracheid development are as follows: the more or less regular thickening of the wall; the loss of cell contents; and the lignification of the wall. It should not be assumed, because a parenchyma cell undergoes the first steps of the changes which would lead to the formation of a tracheid, that there is any inherent necessity for their continuance. It is perfectly possible that the course of development might be arrested at any point, and that any or all of these changes might be incomplete, according to the usual standards of completeness. Unfortunately, the cases of secondary growth in modern pteridophytes are so few in number and so limited in extent that there are very few opportunities for comparison; but this very thing—the incomplete development of the tracheids—has been described as characteristic of the secondary xylem of other pteridophytes, and indeed is almost made the test of secondary xylem.

BOODLE (**1**), in his account of the secondary thickening in the roots of *Ophioglossum vulgatum*, figures both a cross and a longitudinal section of secondary tracheids, which he describes respectively as a "developing tracheid with its protoplasmic contents" and as a "longitudinal section showing part of the xylem with one developing tracheid containing protoplasm and a nucleus." In both these cases the tracheid character of the cell is too pronounced to be questioned. In the case of *Angiopteris evecta*, HILL (**14**) says with reference to the secondary growth: "Semi-lignified elements with protoplasmic contents are found on the inside of the meristem."

If seems strange indeed, that while, in the case of other pteridophytes, it is taken as a matter of course that tracheids may retain part of their protoplasmic contents and appear in various stages of development, in Isoetes the same condition has been looked upon as an insuperable objection to the tracheid character of the cells in question. It is obviously much more natural to interpret this tissue as a case of arrested development, than to regard it as anything so extraordinary as a combination of xylem and phloem. The fact that we find cases of immature and imperfectly developed secondary xylem in other pteridophytes is more enlightening as a basis of interpretation than is the presence of anomalous secondary thickening in the far-removed Dracaena.

The irregular disposition of the thin areas in the pitted tracheids, while not usual in the pteridophytes, is probably more common than has been supposed. GWYNNE-VAUGHAN (**11**), in his recent work on the tracheae of ferns, calls attention to the irregularities in the Osmundaceae, Botryopteris, and others, illustrating cases of distinctly pitted walls. FARMER and FREEMAN (**10**) describe a range of structure in the xylem of *Helminthostachys zeylanica* from tracheids "with characteristic bordered pits of an oval or even circular form" to those "in which the pits assimilate to the more scalariform type met with in the majority of ferns." In Lycopodium in the primary xylem the thin areas are mostly long and narrow, of the scalariform type, but in the slender tracheids they may be round or oval, giving the tracheid a mottled or pitted appearance. A study of the apices of stems of Lycopodium affords an opportunity for a comparison of phloem and young tracheids, a comparison which is of interest as throwing light on the nature of the pitted cells of Isoetes. In the apices of Lycopodium, where the xylem is not yet mature, it is not difficult to find tracheids that have round or oval pits, and which before they are lignified present a similar appearance to that of the pitted cells of Isoetes. In fact, in *L. pithyoides*, the fully developed sieve cells and the pitted tracheids in which lignification has not yet taken place differ only in the greater regularity of the pitting of the tracheids. If the development of the more slender tracheids of Lycopodium were arrested before lignification had begun, it would be difficult to distinguish sieve cells from tracheids except by position, since both have so nearly the same general appearance and the same reactions to stains. As the disposition of the thickening of the primary tracheids of Isoetes is much less regular than in other pteridophytes, it might reasonably be expected that the secondary xylem would also show irregularities.

One of the reasons given by RUSSOW and subsequent observers for regarding the "prismatic layer" as part phloem, is that it is in direct continuity with the phloem of the leaf traces. I am not disposed to question the nature of the phloem either in the leaves or roots. There is nothing in its position and structure to cause any hesitation about accepting it as phloem. The sieve tubes possess well-defined sieve plates, and the tissue as a whole is so definitely marked off, both in position and development, from the xylem and all adjacent tissues, that there is no apparent reason for questioning its identity as phloem.

There can be no question of the continuity of the old leaf traces and the "prismatic layer" in such cases as are shown in *figs. 19, 20*; but in the case of young leaf traces the point is not so certain. The indications are that the continuity is a result of the overgrowth of the leaf traces by the secondary tissues. *Fig. 17* is a diagram which illustrates a thing that occurs in some if not in all cases where such a continuity exists. In any old stem there are present a very large number of leaf traces, of which only a comparatively few at the top are alive and active. The upper part of the stem is a meristematic region, composed of the meristematic leaf traces and the zone whose lower projection is the cambium. This region is indicated in the diagram by fine dots. The xylem strands of the various leaf traces of that level move in together, forming a more compact region, the vascular axis. The phloem ends in the parenchyma, three or four cells from the vascular axis, in the region in which the cambium has not yet become defined. As the meristematic region becomes localized, forming the cambium, the parenchyma with which the leaf trace phloem is connected is pushed out farther and farther from the vascular axis by the secondary tissues. The phloem can retain its continuity with this region in three ways: the xylem at the base of the leaf may elongate sufficiently to compensate for the secondary growth in that region; there may be a splitting-apart of the tissues of the bundle, permitting the phloem to slide along the xylem; or the phloem of the leaf trace will be torn apart, leaving one end connected with the "prismatic layer" while the other is carried out into the cortex. Undoubtedly, while the leaf trace is young, there is an adjustment by the first method. It should be noted, however, that the leaf traces which are connected with living leaves are comparatively few in number and are found in that part of the stem in which secondary growth is scarcely observable. At some time in the development of each leaf trace there comes a time when it is no longer capable of extension and is unable to keep pace with the development of the stem. At this point the tissues of the leaf trace give way, and the outer part is carried out into the cortex and finally sloughed off, while the base becomes more or less crushed and remains as a dead stump, which in time may be completely buried in the secondary wood.

While the conditions which have led to the imperfect development of the vascular tissues cannot be known with certainty, among them are doubtless the aquatic habit and the reduction or shortening of the stem. The anatomy of Isoetes does not seem to indicate, as SMITH says (p. 324), "that the genus Isoetes represents a more primitive type of sporophyte than any other vascular plant," but it supports the view of SCOTT that "the group has clearly undergone reduction from some more complex type, and probably from some highly organized form of lycopod, as indicated by the secondary growth, the marked heterospory, and the somewhat complex organization of the leaves and the root-bearing portion of the axis." As a consequence of a shortening or any reduction in stem development, there would naturally be a reduction in the xylem. This might be either in the amount of the xylem, even to the extent of the entire disappearance of the secondary wood, or there might be a reduction in the development of the xylem. In the other modern pteridophytes it is apparently the former which has taken place, secondary xylem appearing rarely and in small amounts; and, as HILL (15) infers from a comparison of the examples of pteridophytes showing the phenomenon, it is more probably an example of reduction than a new development. In Isoetes, however, the reduction in the bundle has not been limited to the xylem portion, but has extended to the whole of the phloem, both primary and secondary.

The position of Isoetes

The phylogenetic connections of Isoetes have been discussed in all recent papers, with the great weight of evidence in favor of a lycopod ancestry. The evidence as to its relationship afforded by its anatomy has been taken up recently by BOWER (2), on the basis of the interpretation given by SCOTT and HILL, with the conclusion that Isoetes is in its anatomy a lycopod, with a stem structure which can be explained by regarding it as a stunted lycopod. In his eagerness to show a unity of structure in the Lycopodiales, BOWER makes the following statement (p. 339): "Throughout the Lycopodiales the foliar traces are inserted peripherally, and with only a slight local disturbance upon the periphery of the cauline xylem core." In view of the questionable existence of a cauline portion in the xylem core, there seems to be little justification for so sweeping a statement. It is in this very thing that Isoetes differs markedly from other adult lycopods, although the difference is not of such a character as to make the relationship doubtful. The difference is correlated with the stunted habit, and such differences of body habit have never been admitted to have great weight in determining the larger groupings. The stunted habit of stem is not limited in Lycopodiales to Isoetes, but it occurs also, though of very different type, in Phylloglossum.

Even among those who recognize the strong lycopod affinities of Isoetes, it is suggested occasionally that it might be advisable to separate Isoetes from the lycopods and establish a new order, Isoetales. The present tendency seems to be toward a multiplication of orders, so that it may be well to consider the desirability of it in this case.

The closest connection of Isoetes is, as has been frequently pointed out, with the Lepidodendreae, although it has many points in common with modern lycopods. The spore-producing members, in structure and development, are unquestionably of the lycopod type, and as such present no obstacle to the retention of the group in the Lycopodiales. With reference to the anatomy my work would seem to strengthen the position of Isoetes in the Lycopodiales. The irregularities of its structure are not of such a nature as to isolate the group. Aside from the possible lack of a cauline portion in the stele, the irregularities of its anatomy are limited to the absence of primary phloem in the stem; the absence of secondary phloem; the lack of differentiation into protoxylem and metaxylem in the stem; the large amount of parenchyma in the secondary wood; and the imperfect development of the wood.

The absence of primary phloem seems to be characteristic of Isoetes. There are no indications of it in the four species described in this paper, and SCOTT and HILL say of *I. Hystrix* "that it is not possible to identify primary phloem with certainty." Although the absence of primary phloem is recorded for juvenile pteridophytes (e.g. *Matonia pectinata*) by TANSLEY and LULHAM, (**23**, p. 482), so far as is known it is present in the stem of all other adult pteridophytes. In this point, then, Isoetes stands alone. The presence of phloem in the leaf traces and roots, and the collateral arrangement of the bundle in the lower part of the leaf trace indicates a descent from a line in which the phloem is present in the stem as a layer around the xylem. It is difficult to tell what importance to attach to the tendency of the leaf trace to become concentric in the middle and upper part; and to the occasional occurrence of mesarch xylem in the leaf trace.

In regard to the next point, the absence of secondary phloem in a stem with a cambium, the isolation of Isoetes is less certain. SCOTT (**20**, p. 167) in discussing the secondary growth of the Lepidodendreae says: "Although the presence of primary phloem can be recognized with certainty, some doubts have been expressed as to the production of secondary phloem by the cambium." It may be well to remember, too, that there are cases among the modern pteridophytes in which secondary xylem is produced, but no secondary phloem has been observed. This suggests that when reduction occurs in a form with secondary thickening, the disappearance of the phloem precedes that of the xylem.

The next peculiarity of the stem anatomy, the absence of differentiation into protoxylem and metaxylem in the vascular axis, is so obviously related to the stunted habit of the stem that it contributes nothing to a discussion of the position of Isoetes.

In the peculiarities of the structure of its secondary wood, Isoetes finds its nearest prototype in certain Lepidodendreae, as has been pointed out by previous writers. The forms which present the greatest similarity of structure are *Lepidophloios fuliginosus* and *Lepidodendron obovatum*. According to SCOTT (**21**) the cambium in *Lepidodendron obovatum* produces parenchyma only and no tracheids; but the cambium in *Lepidophloios fuliginosus* produces either secondary parenchyma only, or secondary parenchyma in which are imbedded groups of tracheids. Certain species of Isoetes present a close approximation to both conditions. In some species the secondary xylem is almost wholly parenchymatous, with no well-formed tracheids and only a few immature tracheids. In other cases there are groups of tracheids associated with the parenchyma, and in addition a certain amount of immature tracheid tissue. Isoetes accordingly differs from these two members of the Lepidodendreae only in the presence of immature tracheids in the secondary xylem. It is not improbable that future work in the Lepidodendreae may bring to light a similar situation in that group.

In point of anatomy, then, there seems to be no adequate ground for the separation of Isoetes from the Lycopodiales.

The strongest argument for the establishment of a separate order has been drawn from the gametophyte generation, in the presence of a multiciliate sperm. While this is a character of great importance, we should consider the extent of our evidence before attaching too much weight to it. It must not be forgotten, moreover, that lycopod sperms occasionally depart from the biciliate type. BRUCHMANN (**4**, p. 32) speaks of the occasional occurrence of sperms with three cilia in *Lycopodium clavatum*. If we reflect that our knowledge of the sperms of the modern genus Lycopodium is limited to those of a few species, and that we have no knowledge at all of the sperms of the more closely related Lepidodendreae, we may be less inclined to regard the character of the sperms as preponderant in determining the position of Isoetes.

Summary

1. The vascular axis is a non-medullated monostele, composed of tracheids and parenchyma. There is no differentiation into protoxylem and metaxylem.

2. There is no primary phloem in the stem. It is found in the leaf traces and root bundles only.

3. The cambium gives rise to cortex on the outside and secondary xylem on the inside. The so-called "prismatic layer" is secondary xylem. The cambium does not form phloem.

4. The secondary xylem consists of various combinations of the following types of cells: (*a*) Spiral and annular tracheids. (*b*) Immature tracheids, slightly lignified, with irregular rings or spiral thickenings. (*c*) Immature tracheids, unlignified, nucleate or enucleate, with irregular rings or spiral thickenings. (*d*) Immature tracheids, nucleate or enucleate, with slightly thickened, pitted walls. (*e*) Parenchyma cells, which may have little protoplasm and small nuclei, or abundant protoplasm and large nuclei.

5. The secondary xylem of *I. Nuttallii* shows zonation. *I. echinospora* var. *Flettii* and *I. Tuckermani* var. *Harveyi* do not. *I. melanopoda* shows it occasionally in old stems. Starch does not occur in the secondary xylem except in the parenchyma zones of *I. Nuttallii.*

6. The root bundles are collateral and monarch. The protoxylem is found on the side away from the phloem and toward the center of the stem, i. e., it is endarch.

7. The leaf traces are collateral, but tend to become concentric in the middle and upper part of the leaf. Thy xylem portion undergoes great reduction above the sporangium, but the phloem is not reduced correspondingly. The sieve plates are transverse.

8. Near the vascular axis the leaf trace does not show differentiation into protoxylem and metaxylem. In the outer part of the cortex and in the region of the sporangium it is usually exarch. In *I. Nuttallii* it is occasionally mesarch above the sporangium and in the region of the sporangium.

This investigation was conducted at the University of Chicago under the direction of Professor JOHN M. COULTER and Dr. W. J.

G. LAND, of whose advice and encouragement I wish to express my keen appreciation.

MOUNT HOLYOKE COLLEGE
SOUTH HADLEY, MASS.

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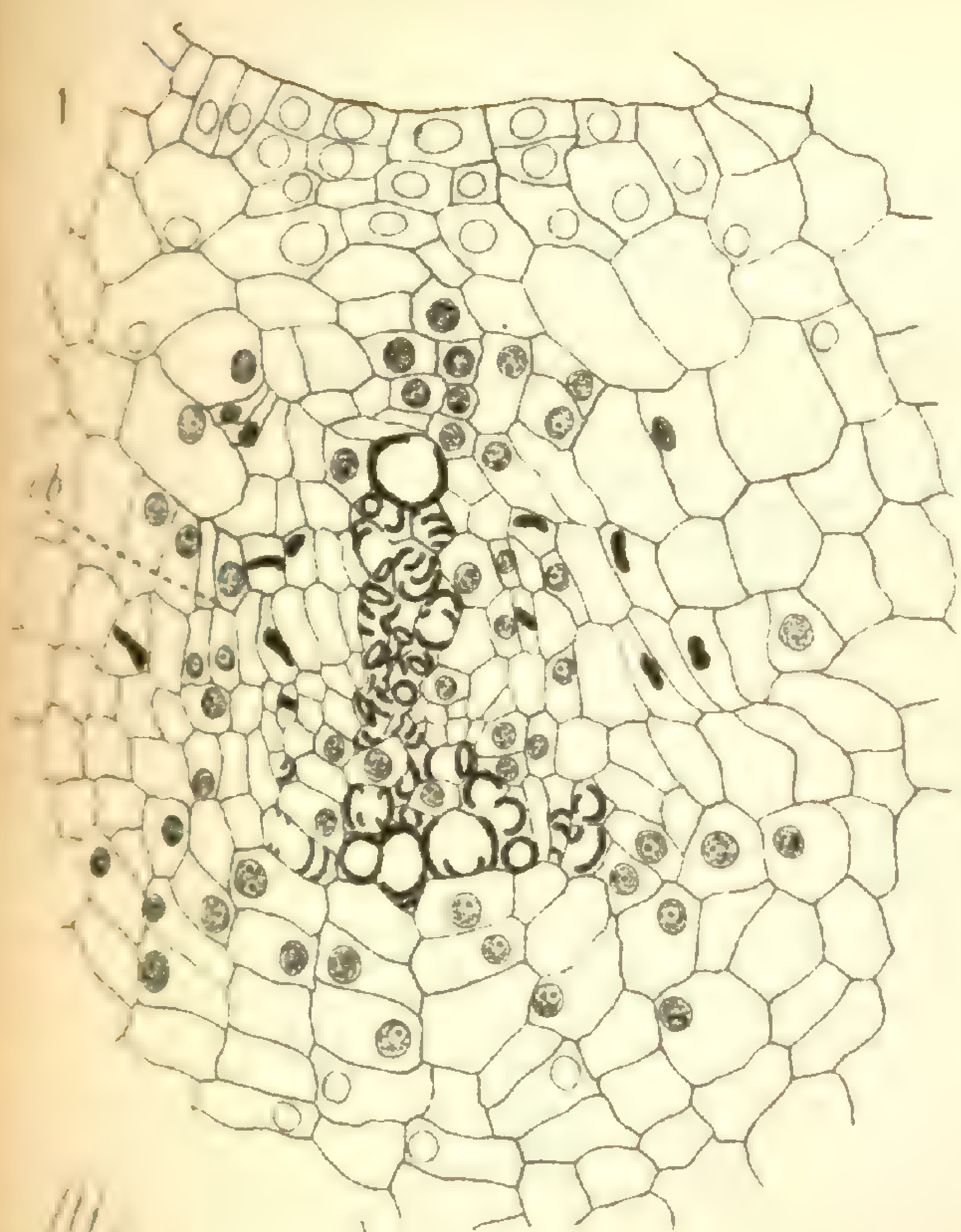

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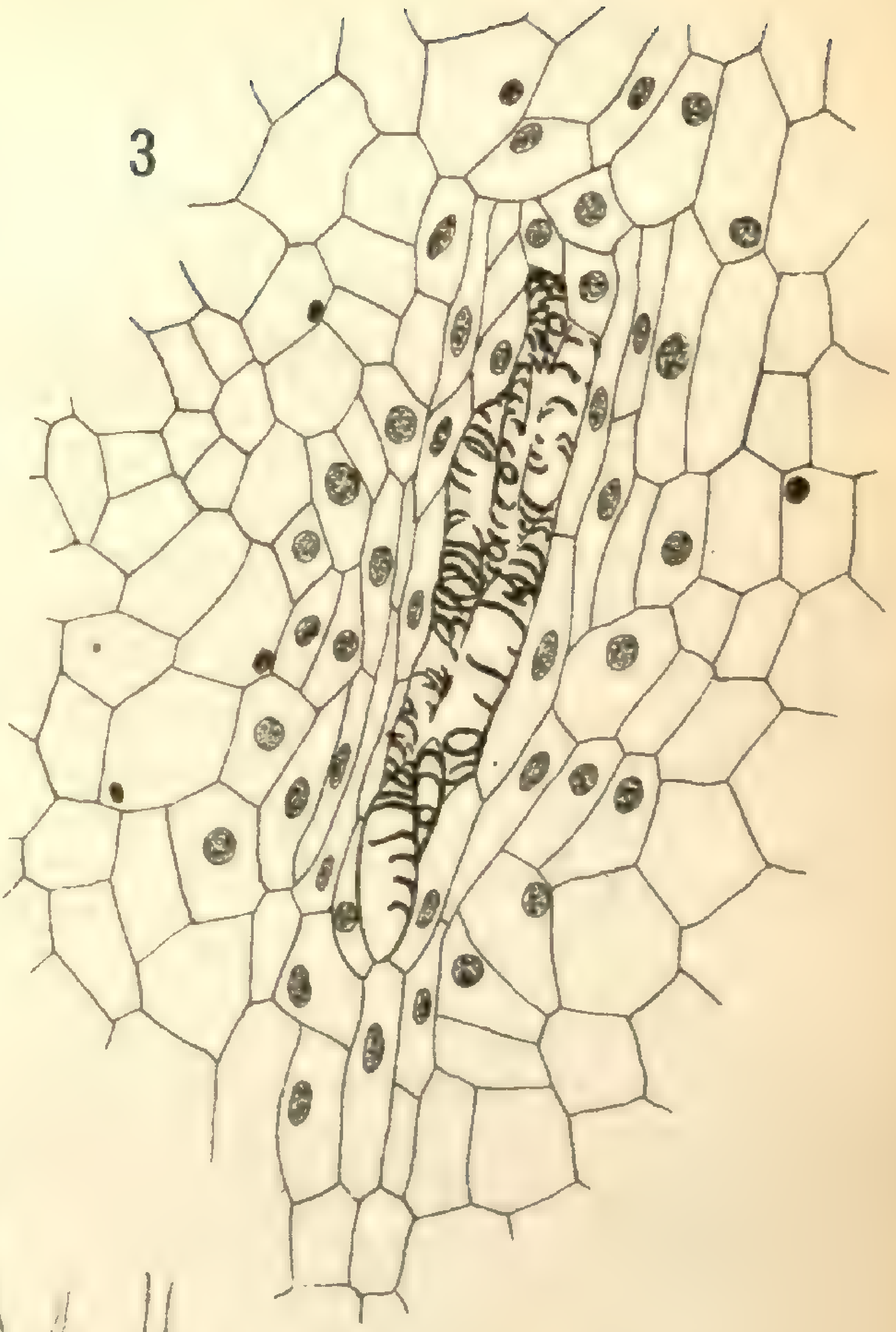

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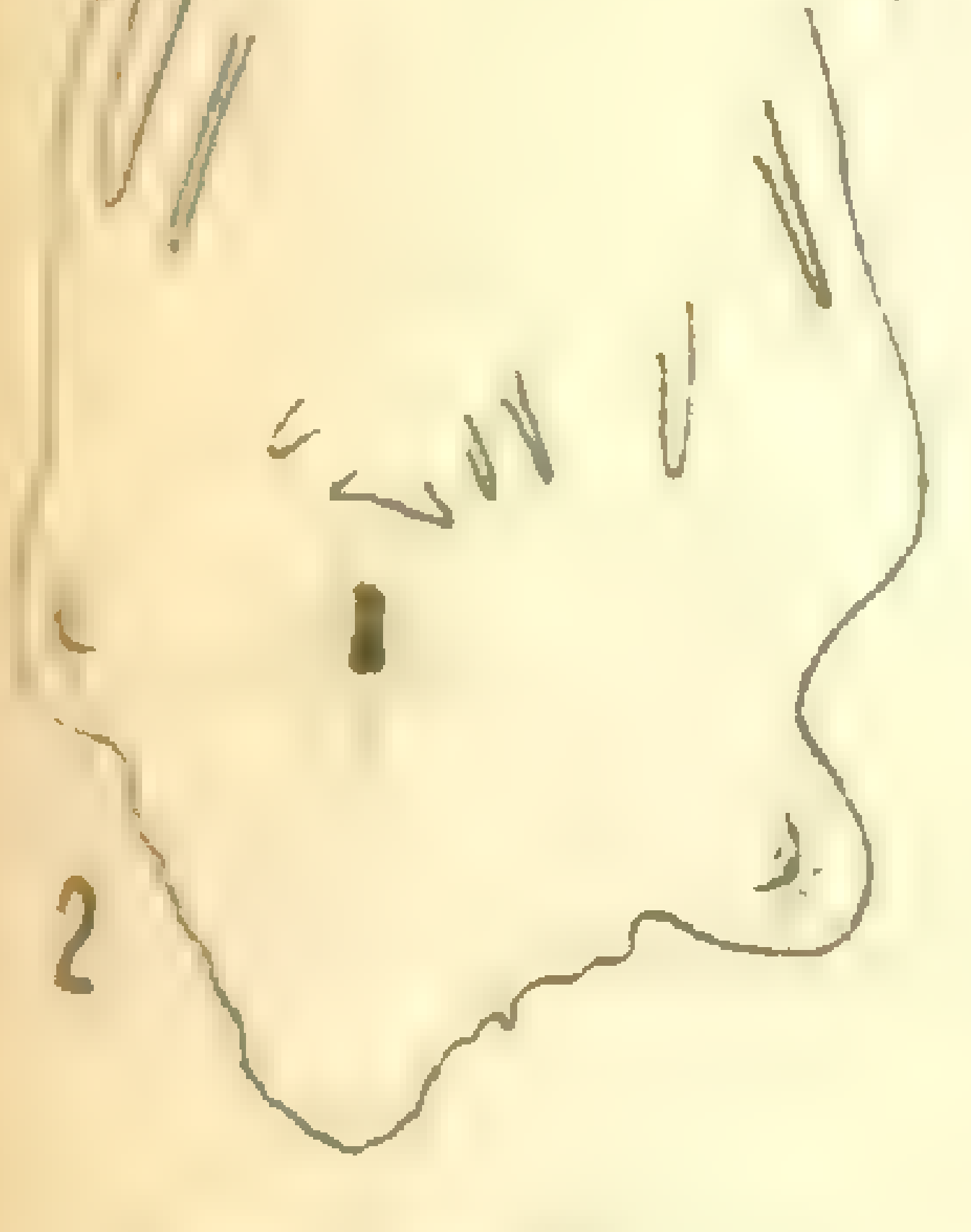

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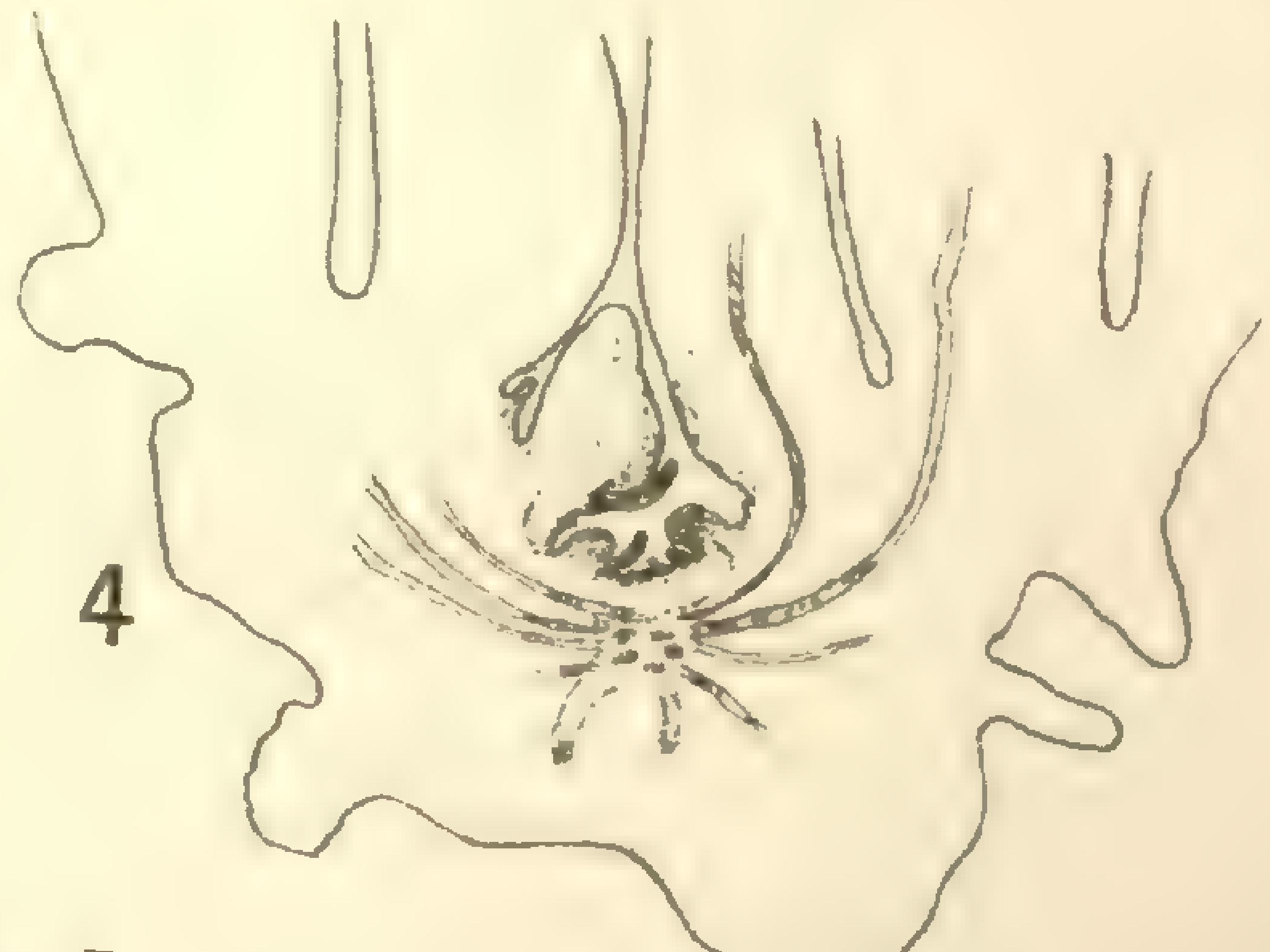

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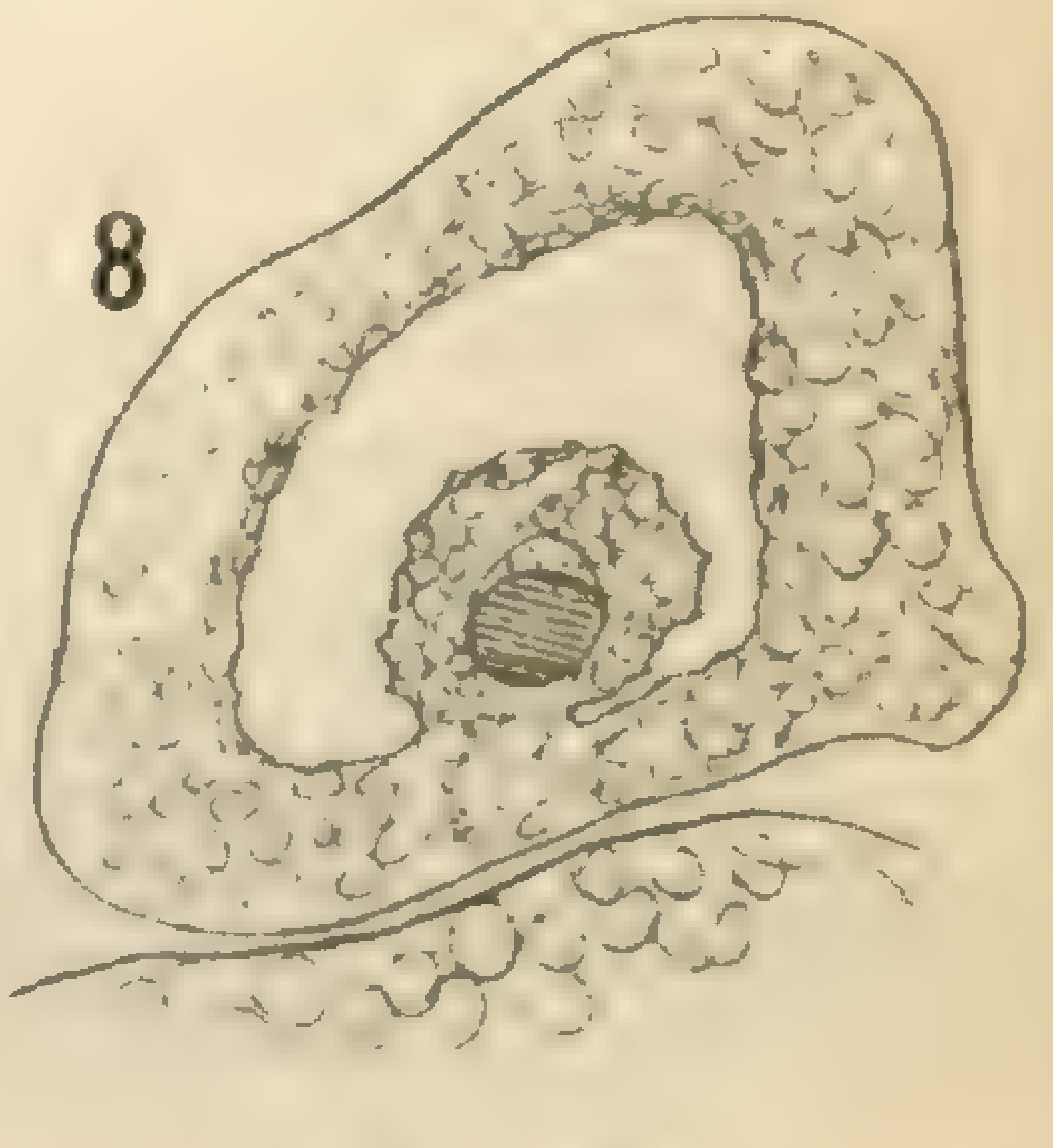

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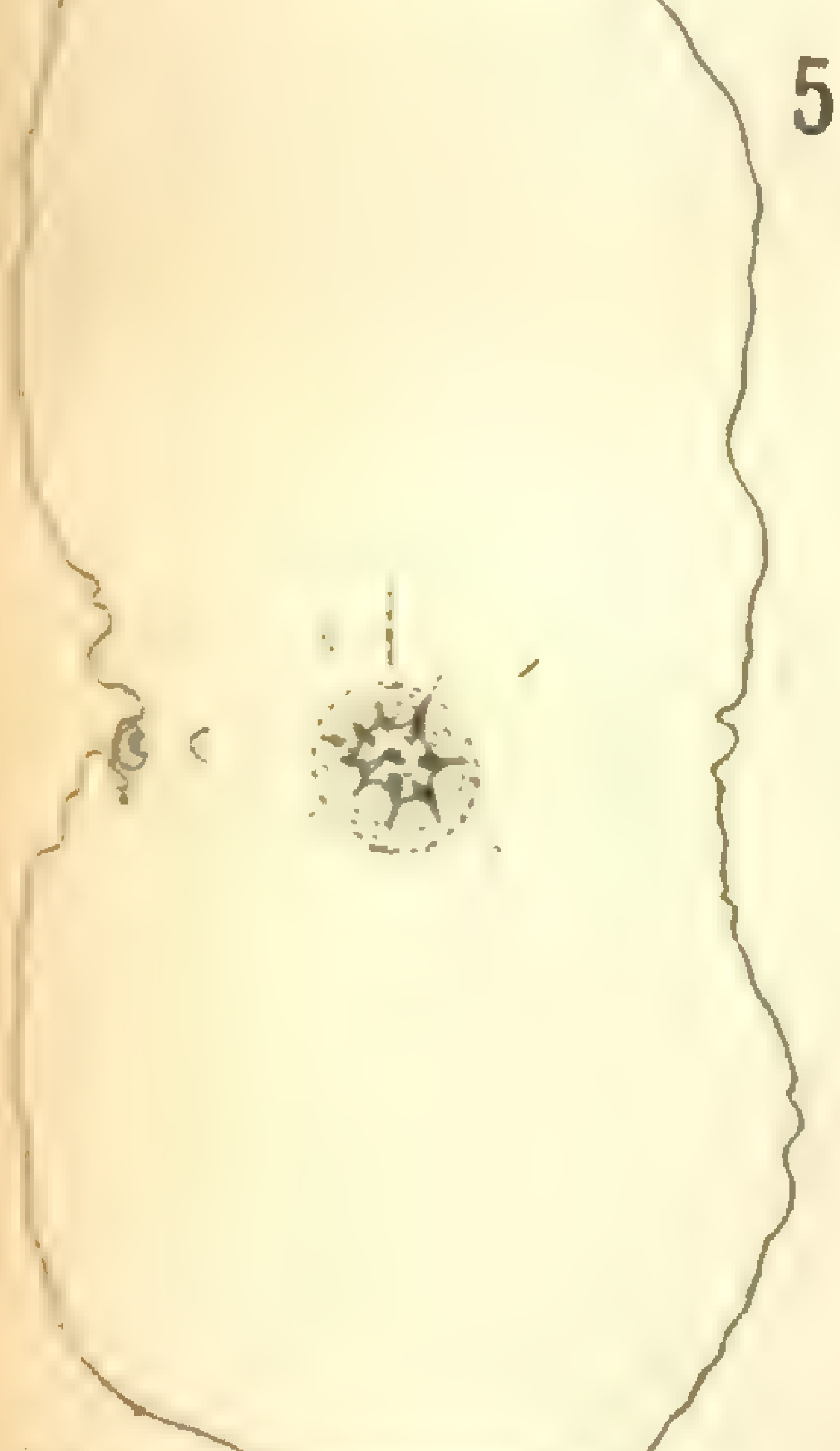

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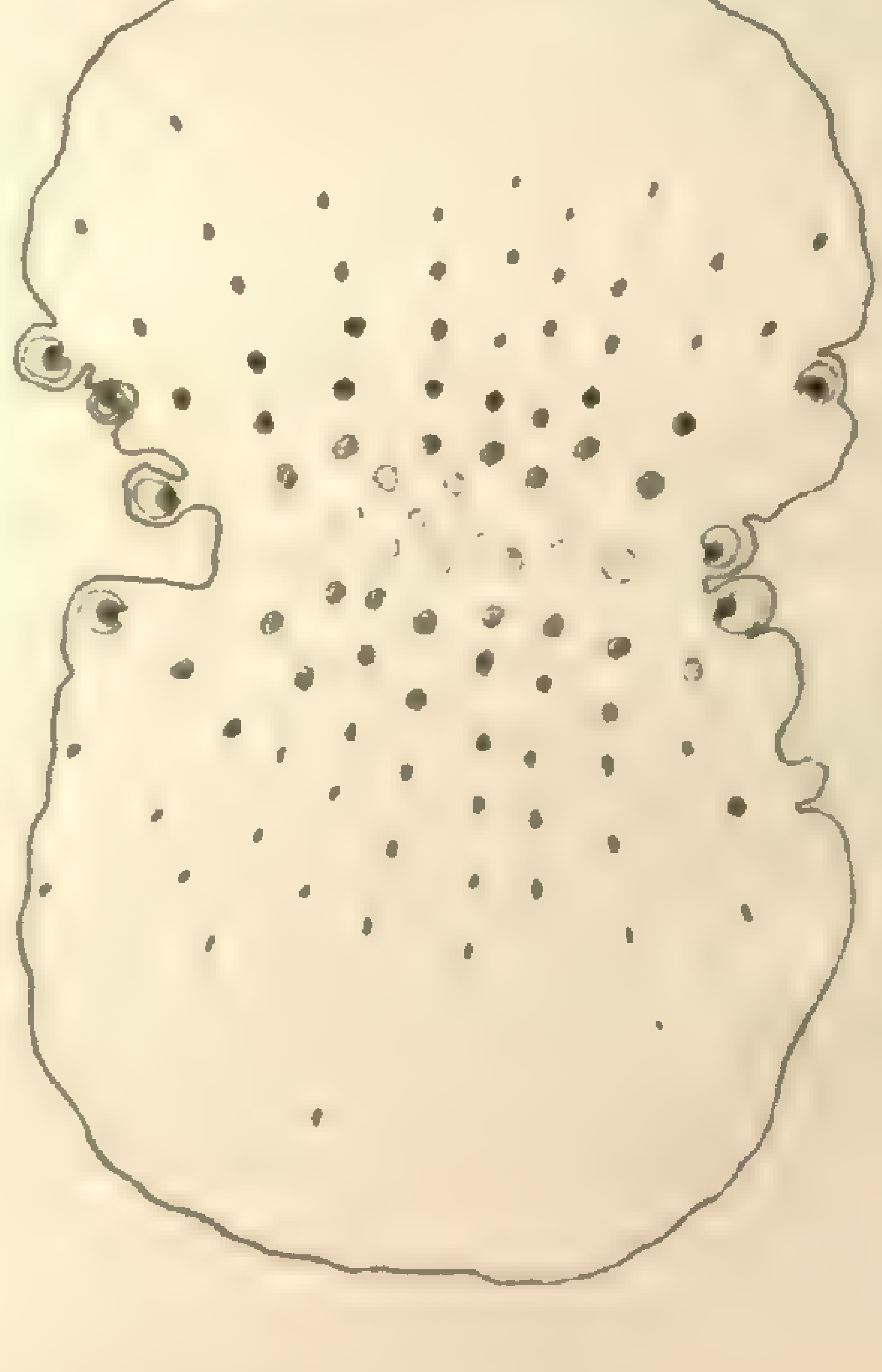

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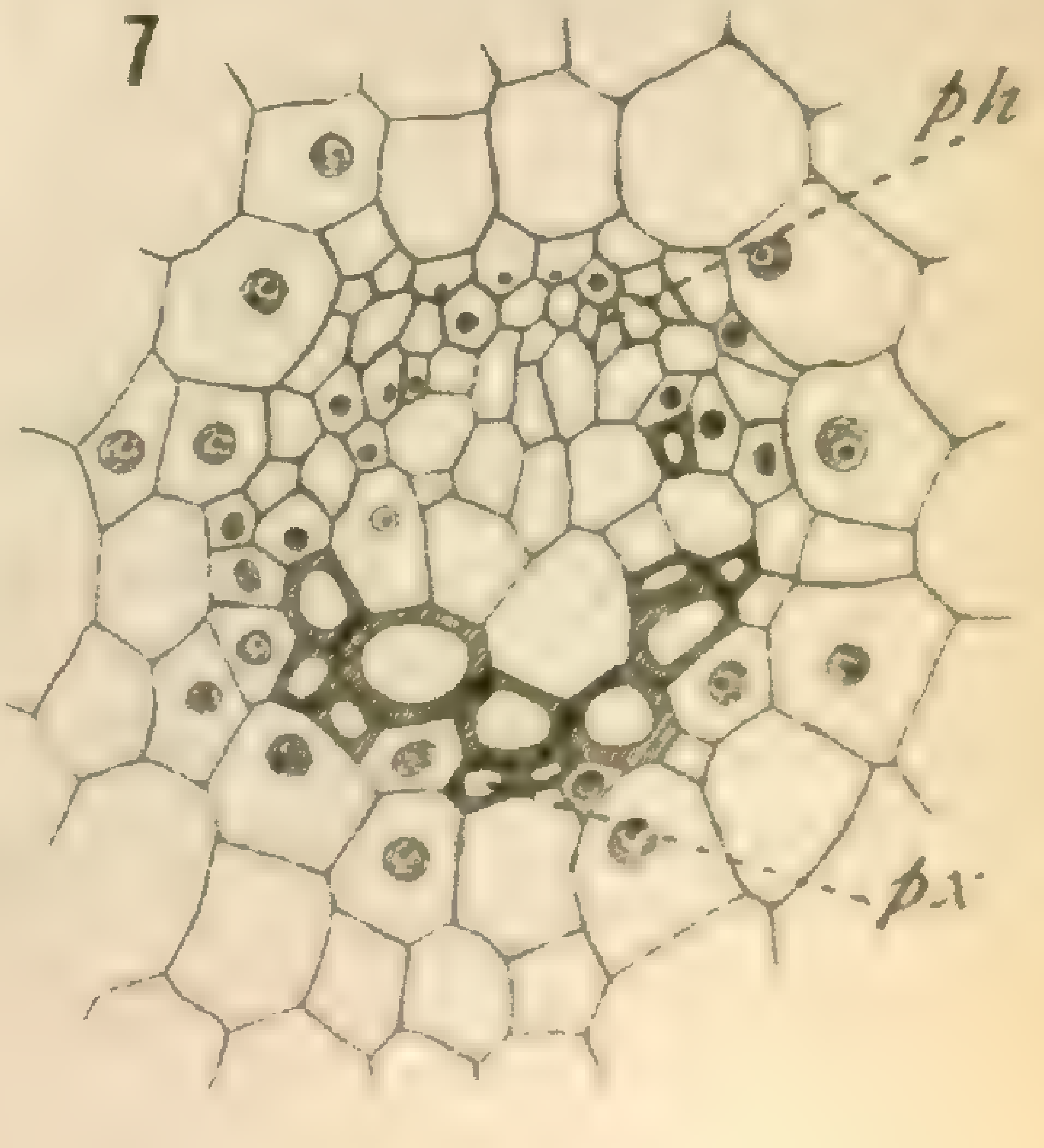

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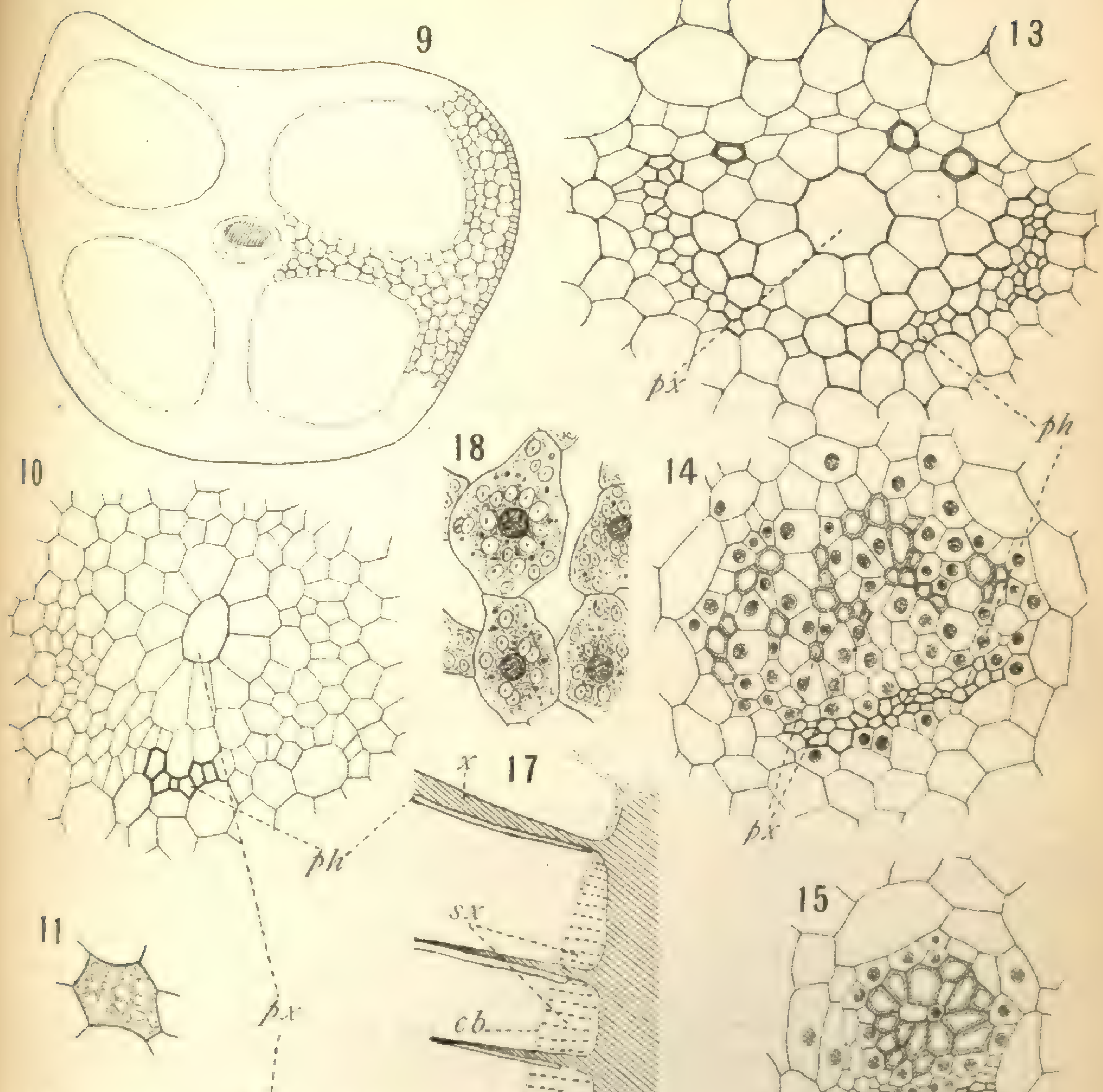
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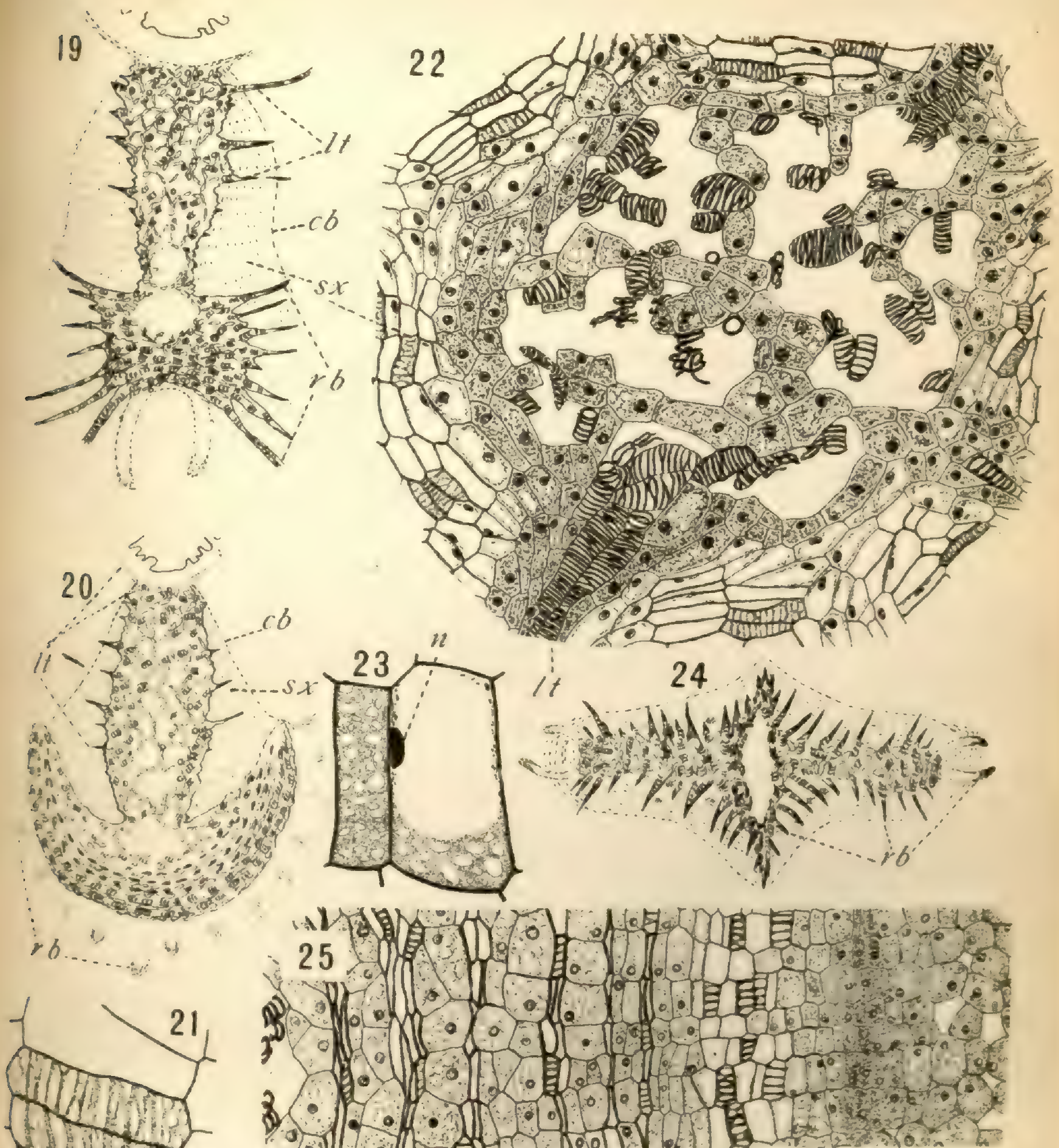
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EXPLANATION OF PLATES XIX–XXI

PLATE XIX

Figs. 1–4.—I. echinospora var. *Flettii. Figs. 5–8.—I. melanopoda*

FIG. 1.—Longitudinal section of the stele of young plant cut in the plane of the furrow. ×380.

FIG. 2.—Longitudinal section of the stem of young plant cut in the plane of the furrow. ×37.

FIG. 3.—Cross-section of the stele of a young plant. ×380.

FIG. 4.—Longitudinal section of a young plant cut across the furrow. ×22.

FIG. 5.—Cross-section of the stem of old plant in the leaf-trace region. ×6.

FIG. 6.—Cross-section of stem below the stele showing root bundles in the cortex. ×6.

FIG. 7.—Cross-section of root bundle before it has left the stem. ×380.

FIG. 8.—Cross-section of mature root. ×48.

PLATE XX

Figs. 9, 10, 12–16.—I. echinospora var. *Flettii. Fig. 11.—I. Nuttallii*

FIG. 9.—Cross-section of mature leaf near the middle. ×37.

FIG. 10.—Cross-section of bundle of young leaf near the tip. ×380.

FIG. 11.—Sieve plate from sieve tube. ×810.

FIG. 12.—Cross-section of bundle of a young leaf near the middle. ×380.

FIG. 13.—Cross-section of bundle of mature leaf cut just above ligule. ×380.

FIG. 14.—Cross-section of leaf trace in cortex just below base of leaf. ×260.

FIG. 15.—Cross-section of leaf trace in cortex half-way between leaf and vascular axis. ×380.

FIG. 16.—Cross-section of leaf trace near the vascular axis. ×380.

FIG. 17.—Diagram to illustrate the relation of leaf traces to secondary wood.

FIG. 18.—Cells of cortex with starch grains. ×380.

PLATE XXI

Figs. 19, 20, 22.—I. echinospora var. *Flettii. Figs. 21, 24, 26.—I. melanopoda*
Fig. 25.—I. Nuttallii. Fig. 23.—I. Tuckermani var. *Harveyi*

FIG. 19.—Longitudinal section of vascular bundle of old plant cut across the furrow. ×22.

FIG. 20.—Longitudinal section of vascular bundle of old plant cut in the plane of the furrow. ×22.

FIG. 21.—Tracheids from secondary xylem at different stages of development. ×810.

FIG. 22.—Cross-section of vascular axis of old plant. ×175.

FIG. 23.—Tracheids from secondary xylem; the cell on the right is sectioned obliquely. ×810.

FIG. 24.—Cross-section of vascular axis through the root region; the long axis is in the plane of the furrow. ×22.

FIG. 25.—Cross-section of stem from the edge of the primary xylem to the cortex, showing zonation in secondary xylem. ×450.

FIG. 26.—Cross-section of the stem from the edge of the primary xylem to the cortex. ×350.

CURRENT LITERATURE

BOOK REVIEWS

Evolution of the filicinean vascular system

Professor Tansley[1] has done well to gather under one cover his lectures on the vascular system of ferns, previously published in the *New Phytologist.* The attempt is made "to gather together the results that have accrued from the researches on the morphology of the vascular system of ferns which have been undertaken during the last few years, and to present these results from an evolutionary standpoint." The first lecture discusses various theories which have been advanced to account for the origin of the main phyla of Pteridophyta. The author favors the view of a direct derivation from Algae in which an alternation of generations had already been established. Accordingly, the sporophyte of pteridophytes would not correspond to that of bryophytes, in which an antithetic alternation of generations seems to have been worked out. The author admits that the presence of an archegonium in both mosses and ferns is an obstacle to this view. Assuming a monophyletic origin for pteridophytes, the view is advanced that the ancestral form was one with a radially organized axis having branches, some of which became specialized as leaves. These leaves were relatively large, and appear to have branched dichotomously; hence the derivation of Filicales from a lycopod form is not credited. It is even suggested that small-leaved forms, such as Lycopodium, may have been derived by reduction from megaphyllous ancestors. The whole scheme of phylogeny proposed is largely speculative, but such attempts will be welcomed by those who find difficulty in accepting **Bower's** well-known hypothesis.

In the second lecture the Botryopterideae are reviewed, and much scattered information on this group is rendered available. Proceeding from the protostelic condition exhibited by Grammatopteris, the complications shown by Zygopteris and other genera are discussed, and the conclusion is reached that this group stands near the ancestors of the different phyla of fern-like plants. Among the Hymenophyllaceae the mode of exit of the leaf-traces lends support to the author's view of the identical nature of leaf strand and stem stele. In discussing this family, as well as the Gleicheniaceae and Schizaeaceae, **Boodle's** work is freely drawn upon and is presented from the evolutionary standpoint. Phylogeny as indicated by the stele is compared with that inferred from the sporangia, and a general correspondence is claimed, though the latter criterion is considered to be the more reliable.

In the sixth lecture the evolution of a protostele into a solenostele (siphonostele) is considered with reference to the examples found in the foregoing families.

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[1] TANSLEY, A. G., Lectures on the evolution of the filicinean vascular system. New Phytologist reprint no. 2. Paper. 8vo. pp. 144. Cambridge: The Author. 1908. 38*s*. 6*d*.

Although no explicit statement is made, the reader is apparently left to infer that there are two modes of origin of a hollow stele: (1) one in which the central tracheids are replaced by parenchyma (Schizaea), (2) one in which fundamental tissue passes into "pockets" at the leaf gaps and becomes continuous with the tissue in contiguous pockets (Alsophila). Although the latter view of the origin of "pith" is essentially that of JEFFREY, no mention of the fact is made in the text, but such reference is relegated to the preface, where the author disclaims adherence to this view. The evolution of solenostely into dictyostely, and finally into polycycly is clearly traced, and the complicated condition found in Marattiaceae is adequately illustrated by diagrams from various sources.

Concerning the Osmundaceae, the conclusion is reached that the stele does not represent a reduced type, but shows a gradual progression from the condition seen in Botryopterideae, from which group the Osmundaceae have probably been derived. The recent work of KIDSTON and GWYNNE-VAUGHAN on fossil members of the group is quoted in defense of this position.

In a succeeding lecture the evolution of the leaf-trace is outlined, and it is shown that elaborations of the primitively simple curved trace follow upon increase in the leaf-surface, and in turn bring about increasing complexity in the central cylinder of the stem. According to the author's view "the leaf-trace leads, and the stele follows, in the course of evolution." The ontogeny of the vascular system is next summarized, and a final lecture is devoted to a comparison of the vascular system of various phyla. The criticisms of JEFFREY's primary groups Lycopsida and Pteropsida have already been dealt with in this journal[2].—M. A. CHRYSLER.

The American Breeders' Asssociation

The fourth annual report of the American Breeders' Association[3] is, in a number of features, a decided improvement over previous volumes. The same high standard of matter is maintained as in previous reports, but there is more of it; it is printed on better paper; and contains numerous fine half-tone engravings. Unlike many publications which are more or less influenced by practical considerations, the articles presented in the reports of the American Breeders' Association appear to suffer no diminution of scientific value because of the large contingent of practical breeders among its membership and on its programs. Almost every phase of practical and theoretical breeding of plants and animals, as well as two interesting reports upon eugenics, the new science of improvement of the human race, are included. Papers of importance from the standpoint of the practical plant-breeder include several upon the production of disease-resistance in various plants by W. A. ORTON, P. K. BLINN, and H. L. BOLLEY;

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[2] JEFFREY, E. C. Are there foliar gaps in the Lycopsida? BOT. GAZETTE 46:241–258. *pls. 17, 18.* 1908.

[3] Report of the American Breeders' Association. Vol. IV. pp. 373. *pls. 3, figs. 74.* 1908.

the improvement of apples and other tree and vine fruits, by S. A. BEACH, W. T. MACOUN, and J. A. BURTON; the breeding of cereals by L. S. KLINK and C. E. SAUNDERS; the improvement of hops by selection and breeding by W. W. STOCKBERGER; on cotton-breeding by DAVID COKER, H. J. WEBBER, and D. A. SAUNDERS; the breeding of fiber crops, by J. H. SHEPPARD, L. H. DEWEY, FRITZ KNORR, and H. L. BOLLEY; the breeding of vegetables, by W. W. TRACY; roses by PETER BISSETT, and W. VAN FLEET; tobacco by A. D. SHAMEL, J. B. STEWARD, A. D. SELBY, and W. H. SCHERFFIUS; carnations by C. W. WARD; forage crops by T. F. HUNT and H. S. ALLARD; and forest and nut trees by GIFFORD PINCHOT, W. L. JEPSON, and G. L. CLOTHIER. In all of these articles, as well as in a number dealing with animal breeding, there are many facts recorded which are of more than passing scientific interest. Papers of a more strictly theoretical scientific character are: "Organic correlations," by E. M. EAST, "Some gaps in our knowledge of heredity," by H. J. WEBBER, "The composition of a field of maize," by G. H. SHULL, "Recent advances in the theory of heredity," by C. B. DAVENPORT, "Color factors in mammals," by W. J. SPILLMAN, and "Mendelian phenomena and discontinuous variation," by W. J. SPILLMAN. The wide range of subjects and the almost uniform high excellence of the papers and reports included in this volume show that the American Breeders' Association has a large mission to fill, and that it is filling it creditably. These annual reports are made the treasure-house of all the best things gained in the experience of our foremost practical breeders and students of heredity during the progress of their work. The efforts made by the practical breeders to present their experience in as proper scientific form as possible, and to interpret those experiences in the light of the latest scientific results, and the efforts of the scientific breeders to state their results in as simple, direct, and comprehensible a manner as possible, have a most salutary effect upon all those connected with the American Breeders' Association, and must continue to supply us with the best annual crops of information regarding the factors which enter into the breeder's work, whatever may be his motive in breeding.—GEORGE H. SHULL.

MINOR NOTICES

Sertum Madagascariense.[4]—This paper is based on two collections of plants made in Madagascar, one by JOHN GUILLOT in the district of Vatomandry on the east coast and the other by HENRI RUSILLON on the plateau of Imerina. The first part of the work consists of a brief consideration of the botanical geography; and in the second part the author in collaboration with several prominent European specialists, gives a list of the species. Among the plants recorded 26 species and 4 varieties are described as new to science. The larger and more critical genera are accompanied by analytical keys to the species, and several text-figures have been introduced. A complete index to the vernacular and scientific names is also added. The work is a notable contribution to our knowledge of the flora of Madagascar.—J. M. GREENMAN.

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[4] HOCHREUTINER, B. P. G., Sertum Madagascariense. Ann. Conserv. et Jard. Bot. Genève 11–12:35–135. *figs. 23.* 1907–1908.

North American Flora.[5]—Part 4 of Vol. XXII contains a continuation of Dr. P. A. RYDBERG'S elaboration of the Rosaceae. The groups treated are Potentilla and the related genera. In all sixteen genera are here considered, and to these the author refers 277 species, of which 70, approximately one-fourth, are described as new. Potentilla leads with 176 recognized species, 44 being published as new to science. Two new genera (*Zygalchemilla* and *Lachemilla*) are proposed.—J. M. GREENMAN.

NOTES FOR STUDENTS

Longevity of seeds.—In a long paper[6] EWART classifies seeds according to their duration of life under optimal conditions as: microbiotic seeds, with a longevity of less than 3 years; mesobiotic, with a longevity of 3 to 15 years; and macrobiotic, with a longevity of 15 to 100 years. Most of the paper (175 out of 210 pages) is taken up with a table, drawn from the works of various investigators, showing the age, percentage of vitality, etc., of various stored and buried seeds. EWART says: "Longevity depends not on the food materials or seed coats, but upon how long the inert protein molecules, into which the living protoplasm disintegrates when drying, retain the molecular grouping which permits of their recombination to form the active protoplasmic molecule when the seed is moistened and supplied with oxygen." Longevity, however, he holds, is in general found in seeds with seed coats impervious to water, and asserts that this impermeability is due to cuticular structures in almost all cases examined. In *Adansonia digitata*, on the other hand, all layers of the coats are equally resistant to water.

He agrees with CROCKER that seed-coat characters rather than embryo characters account for the greater number of cases of delayed germination, and he makes considerable use of the data of this writer as evidence on this point. He believes that the longevity of seeds in soil is far less than is generally assumed. The maximal duration of the seeds of certain Leguminosae under optimal conditions is stated to be between 150 and 250 years, and of Malvaceae and Nympheaceae between 50 and 150 years. An appendix by Miss JEAN WHITE gives the structure of the coats of various resistant seeds. The body of the work is marred by a number of inexcusable errors in the statement of the results of other investigators. —WM. CROCKER.

Enzymes.—GRÜSS has suggested[7] a method of capillary analysis of enzymes for which he claims considerable value. It consists in pulverizing a portion of the tissue containing the enzyme in a small amount of glycerin and placing this on a filter paper. From this mass the water circle spreads and the enzymes can be located at various radial distances from the center. In dealing with oxidases the whole process is performed in an atmosphere of hydrogen. It is not evident that this method is of any great value further than as a mere means of demonstrating the presence of certain enzymes. GRÜSS also claims by it to gain evidence that cytase is not distinct from diastase, and believes he has shown in a number of other cases that a single enzyme performs several catalytic functions. His arguments against the specificity of enzymes are to a degree plausible, but are far from conclusive.

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[5] North American Flora, Vol. XXII, Part 4, pp. 293–388. New York Botanical Garden, 1908.

[6] EWART, ALFRED J., On the longevity of seeds. Proc. Roy. Soc. Victoria. N.S. 21:1–20. *pls. 1, 2.* 1908.

[7] GRÜSS, J., Kapillaranalyse einiger Enzyme. Ber. Deutsch. Bot. Gesells. **26a:** 620–626. 1908.

GRÜSS also asserts,[8] on the basis of considerable experimental evidence, that the reducing power of fermenting yeast attributed to the action of reductase can be accounted for by the nascent hydrogen set free by the hydrogenase of the yeast. In the presence of fermenting yeast the reduction of sodium seleniate and sulfur occur as they do when treated with nascent hydrogen. He finds no evidence for postulating reductase in yeast. He believes that the fungi in general possess hydrogenase and not reductase. If this be true the reductions carried on by this group of plants are strikingly similar to the simplest reductions in the chemical laboratory. He agrees that yeast and other fungi show a very slight reducing power not due to hydrogenase, but the substance that produces this slight reduction shows none of the characteristics of an enzyme.—WM. CROCKER.

Germination in Rhinanthaceae.—SPERLICH[9] believes he has demonstrated that the germination of the seeds of the partially parasitic species, *Melampyrum silvaticum*, *M. arvense*, and *Alectorolophus hirsutus*, is greatly hastened by the presence of the host plant. These seeds show a considerable rest period and he concludes that the favorable action of the host is evident only up to the completion of the "after-ripening." A close examination of his data shows that his conclusions do not necessarily follow from them. He always gets a very low percentage of germination and great variations in results from similar cultures. This indicates the presence of some uncontrolled factor. On discussing "after-ripening" he makes no mention of the general connection of delayed and distributed germination with the seed coats, but attributes these phenomena to embryo characters. He apparently has no knowledge of the literature on the subject. One wonders if his results are not merely the measurement of seed-coat effects. He certainly has not demonstrated dormancy in the embryo itself, which is the first step in establishing his main position. The disposition of a number of German investigators to refer the phenomena of "after-ripening" to the mysteries of the protoplasm is to be deplored, especially when a thorough examination of the facts will often furnish a very simple explanation. It must not be forgotten, however.

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[8] GRÜSS, J., Hydrogenase oder Reduktase? *Idem:* 627–630. 1908.

[9] SPERLICH, ADOLPH, Ist bei grünen Rhinanthaceen ein von einen pflanzlichen Organismus ausgehender äusserer Keimungsreiz nachweisbar? Ber. Deutsch. Bot. Gesells **26a**: 574–587. 1908.

that it has been clearly proved that the fungus of the host is necessary for the normal germination of the seeds of many orchids; but even here our knowledge is of little scientific significance until we know the exact method of the action of the fungus, whether its effect is due to the secretion of certain chemical compounds, which aid in water absorption, or to some other influence.—WM. CROCKER.

Chromogens.—TAMMES[19] reports a new chromogen, dipsacan, which is present in all the genera and species of Dipsaceae examined. Dipsacan has many points of resemblance to isatan and indican, yet it shows points of difference from both these, as well as from the pseudoindicans of the Acanthaceae. At temperatures above 35° C., in the presence of oxygen and water, dipsacan is transformed to a blue pigment, dipsacotin. The optimum temperature for this transformation is 100° C. At high temperatures, or at ordinary temperatures through the action of benzin, phenol, or dipsacase, an enzyme of this family of plants, dipsacan is transformed to a yellow-red pigment in the entire absence of oxygen. Upon admission of oxygen this pigment is transformed to dipsacotin.

PALLADIN[11] has already urged that chromogens are universally present in actively respiring portions of plants and that they are products of respiration. TAMMES's results agree with this conception, for dipsacan is found to be most abundant in the most active portions of the plants and in those plants that are in the best condition for growth; otherwise only traces of dipsacan appear.

TAMMES suggests that dipsacan may be a glucoside, and that the yellow-red pigment, which originates independent of oxygen, is one the products of the hydrolysis; but it is not known that sugar is also a product. The formation of the dipsacotin from the yellow-red pigment is a matter of oxidation, as PALLADIN has shown is the case in the production of the pigments from numerous chromogens he has studied. It strikes one as possible that the formation of the chromatic materials in general requires both hydrolysis and oxidation. This would line up all these chromogens with indican.—WM. CROCKER.

Germination and light.—KINZEL[12] publishes another paper on the effect of light on germination of seeds, confirming the results of former papers and adding a number of species to those favored in germination by light.

In a discussion of "after-ripening" he states that the several years' delay in germination shown by the ripe seeds of *Thlaspi arvense* is due to the character of the embryo and not to the character of the coat, for the coat is very delicate. In an article published in 1906,[13] the reviewer has shown that the very marked delay

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[10] TAMMES, TINE, Dipsacan and Dipsacotin, ein neues Chromogen und ein neuer Farbstoff der Dipsaceae. Recueil Trav. Bot. Neerland **5**:—. (pp. 48.) 1908.

[11] PALLADIN, W., Die Verbreitung der Atmungschromogens bei den Pflanzen. Ber. Deutsch. Bot. Gesells. **26a**: 378–389. 1908.

[12] KINZEL, WILHELM, Lichtkeimung. Einige bestätigende und erganzende Bemerkungen zu den vorläufigen Mitteilungen von 1907 und 1908. Ber. Deutsch. Bot. Gesells. **26a**:631–645. 1908.

[13] CROCKER, WM., Rôle of seed coats in delayed germination. BOT. GAZETTE **42**:282. 1906.

in these seeds is entirely due to the coats. The delicacy of the coat is no criterion of its effect, for certainly few seed coats are more delicate than that of the upper seed of the cocklebur, yet it generally secures a delay of a year or more.

It is surprising that experimenters are so slow to see that the proper test for dormancy of an embryo is to free it from incasing membranes with aseptic precautions and then to subject it to germinative conditions. This treatment will probably show the cause of most cases of delay to be in structures surrounding the embryo. If such treatment shows real dormancy of the embryo, as in the radicle of the hawthorn,[14] it is then necessary to find the particular process that is delinquent. This is certainly possible in the light of the great progress that is being made in studying the catalytic nature of protoplasmic activity. When cases of delayed germination are investigated in this way, we may hope for progress. But to assume dormancy is merely marking time and leaves the physiology of delayed germination, as it is now, more than ten years behind other phases of plant physiology.—WM. CROCKER.

Permeability.—RUHLAND[15] holds entirely untenable OVERTON'S theory of the permeability of protoplasm, both in its original form and as modified by NATHANSOHN. In the main RUHLAND offers the same sort of evidence as has ROBERTSON[16] from the animal side. RUHLAND studied the ability of various organic dyes to enter the living cell. Malachite green and thionin, both almost insoluble in lipoids, enter the live cells readily, while rhodamin, highly soluble in lipoids, hardly penetrates them at all. He cites a number of other dye stuffs where just the opposite behavior occurs to that expected by the lipoid theory. Both the acid and basic phthaleins are highly soluble in lipoids. The former penetrate living cells readily while the latter scarcely enter at all. RUHLAND says we have no hint of a reason for this behavior. RUHLAND and ROBERTSON agree that a thin layer of lipoids often exists near the periphery of the protoplasm. They believe, however, that it is not continuous in any case, but only fills interstices of the protein matter. ROBERTSON attributes the permeable character to the nature of the outer, very sparingly soluble, protein layer.—WM. CROCKER.

Reproduction and stimuli.—FREUND[17] has done a rather elaborate piece of work on the effect of external conditions upon the asexual reproduction of Oedogonium and Haematococcus. He finds that previous culture conditions determine very largely the effect of any reagent. Of the several methods he found of producing this response two illustrations will suffice to give an idea of the work. After

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[14] CROCKER, WM., Longevity of seeds. BOT. GAZETTE **47**:69–72. 1909.

[15] RUHLAND, W., Beiträge zur Kenntnis der Permeabilität der Plasmahaut. Jahrb. Wiss. Bot. **46**:1–54. 1908.

[16] ROBERTSON, T. B., On the nature of the superficial layer in cells and its relation to their permeability and to the staining of tissues by dyes. Journ. Biol. Chem. 4:1–34. 1908.

[17] FREUND, HANS., Neue Versuche über die Wirkung der Aussenwelt auf die ungeschlechtliche Fortpflanzung der Algen. Flora **99**:41–100. 1908.

Oedogonium has grown for a considerable time in distilled water in the light, a transfer to darkness or to a dilute nutrient solution causes a development of zoospores. Resting cells of Haematococcus, kept in darkness for some time, produce swarmspores upon being illuminated or supplied with cane or grape sugar.

FREUND finds the chemical nature of the medium rather than its physical or osmotic character the important consideration in the asexual reproduction. In contrast to this, LIVINGSTON found the osmotic character of the media the main consideration in determing the form of Stigeoclonium.—WM. CROCKER.

Phototropic response.—BLAAUW,[18] working with the seedling of *Avena sativa*, concludes that the intensity of the light, multiplied by the least time of exposure necessary to give a phototropic response, is approximately a constant. The intensities used varied from 0.000439 to 26,520 Hefner candles, and the time of exposure from 13 hr. to 0.001 sec. The product of the exposure in seconds by the intensity in Hefner candles averages about 21 and varies from 16.9 to 26.5. This, of course, hardly looks like a constant; but the variation is attributed to the individual differences of the seedlings. The intensity of the light was measured with a Weber photometer, and the observation of the response was made two hours after the end of the exposure. The author says, "The essential condition for the production of a phototropic curvature is the supply of a definite quantity of radiant energy; whether this quantity be supplied in a very short time or extremely slowly, is a matter of indifference."—WM. CROCKER.

Spraying potatoes.—A recent bulletin[19] summarizes the results of the seventh year's work in the ten-year series of potato-spraying experiments begun in New York in 1902. In the ten-year experiments at Geneva, six sprayings increased the yield 39 bushels per acre and three sprayings increased it 29.5 bushels, although both early and late blight were wholly absent and there were but few flea beetles. In fourteen "farmers' business experiments," including 200 acres, the average gain due to spraying was 18.5 bushels per acre; the average total expense of spraying, $4.30 per acre; and the average net profit, $8.53 per acre. In five of the experiments spraying was unprofitable. Eleven "volunteer experimenters" reported gains averaging 66.3 bushels per acre.—F. L. STEVENS.

Alfalfa.—An exceedingly interesting and comprehensive bulletin concerning alfalfa[20] has just appeared from the New York Experiment Station. Among the subjects treated are the following: Varieties grown, uncongenial soil conditions, winter injury, failure of the seed crop, viability of the seed, impure and adulterated seed, fodder, yellow trefoil, weeds. Among the fungous diseases discussed are: Leaf spot, wilt, anthracnose, root-rot and damping off, downy mildew, Ascochyta leaf-spot, Stagnospora leaf-spot, Cercospora leaf-spot, Alternaria disease (?) of seed, frost blisters on leaves, insect enemies, and root-knot; also, as diseases of unknown cause, white spot, yellow top, pitting of the tap-root, and bundle blackening in the tap-root.—F. L. STEVENS.

---

[18] WENT, F. A. F. C., On the investigations of Mr. A. H. BLAAUW on the relation between intensity of light and the length of illumination in the phototropic curvatures in seedlings of *Avena sativa*. Reprint from Proc. Kon. Akad. Wetens. Amsterdam, Sept. 26, 1908. pp. 5.

[19] STEWART, F. C., FRENCH, G. T., and SIRRINE, F. A., N. Y. Agric. Exp. Sta. Bull. 311. January, 1909.

[20] STEWART, F. C., FRENCH, G. T., AND WILSON, J. K., Troubles of alfalfa in New York. N. Y. Agric. Exp. Sta. Bull. 305. November, 1908.

Barium and loco.—In a bulletin on loco weeds[21] CRAWFORD says: "The inorganic constituents, especially barium, are responsible for this action, at least in plants collected at Hugo, Colo. Perhaps in other portions of the country other poisonous principles may be found." *Astragalus mollissimus* and *Aragallus Lamberti* were most fully studied, but other species of these genera, as well as various other genera, have been reported as producing loco.—WM. CROCKER.

Protection against heating.—WIESNER holds that the distribution of green tissues into small leaves or finely divided leaves is a mode of protection against overheating by the sun, and adduces observations and experiments in support therefor.[22] This protection is secured by the small size of the parts which expose a relatively large surface for radiation and at the same time permit many light rays to pass them by.—C. R. B.

Balanced solutions.—OSTERHOUT continues his studies upon balanced solutions with plants,[23] reporting that Na ions, by reducing the toxicity of K, NH_4, Mg, and Ca ions, are an important, and in some marine algae an indispensable, protection. He finds that there is no essential difference between plants and animals in this respect.—WM. CROCKER.

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[21] CRAWFORD, A. C., Barium, a cause of the loco-weed disease. Bur. Plant Ind., U. S. Dept. Agric. Bull. 129. pp. 87. 1908.

[22] WIESNER, J., Versuche über die Wärmeverhältnisse kleiner, insbesondere linear geformter, von der Sonne bestrahlter Pflanzenorgane. Ber. Deutsch. Bot. Gesells. **26a**:702–711. 1908.

[23] OSTERHOUT, W. J. V., Die Schutzwirkung des Natriums für Pflanzen. Jahrb. Bot. **46**:121–136. 1908.

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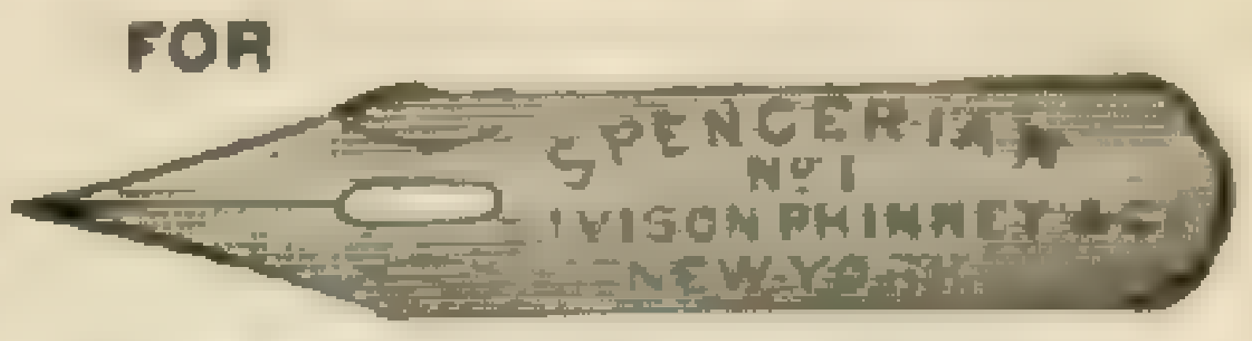

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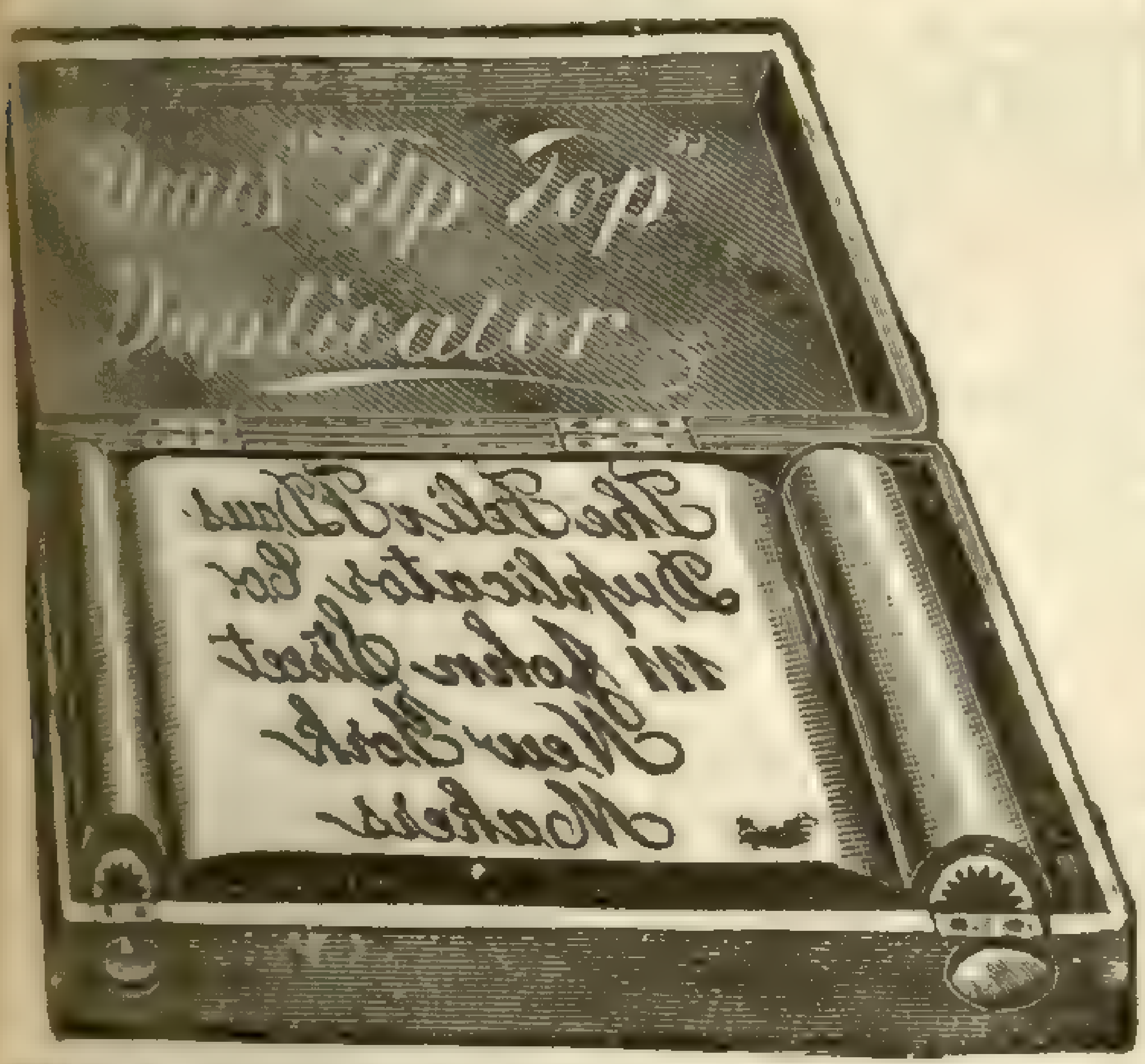
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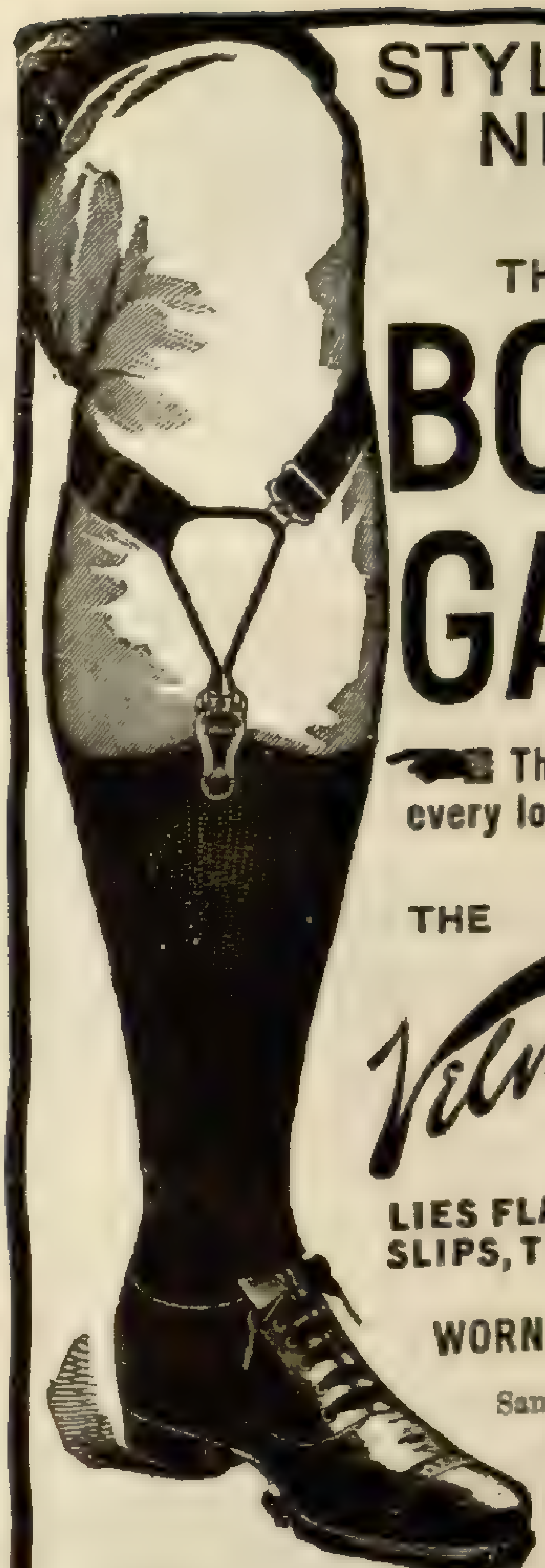

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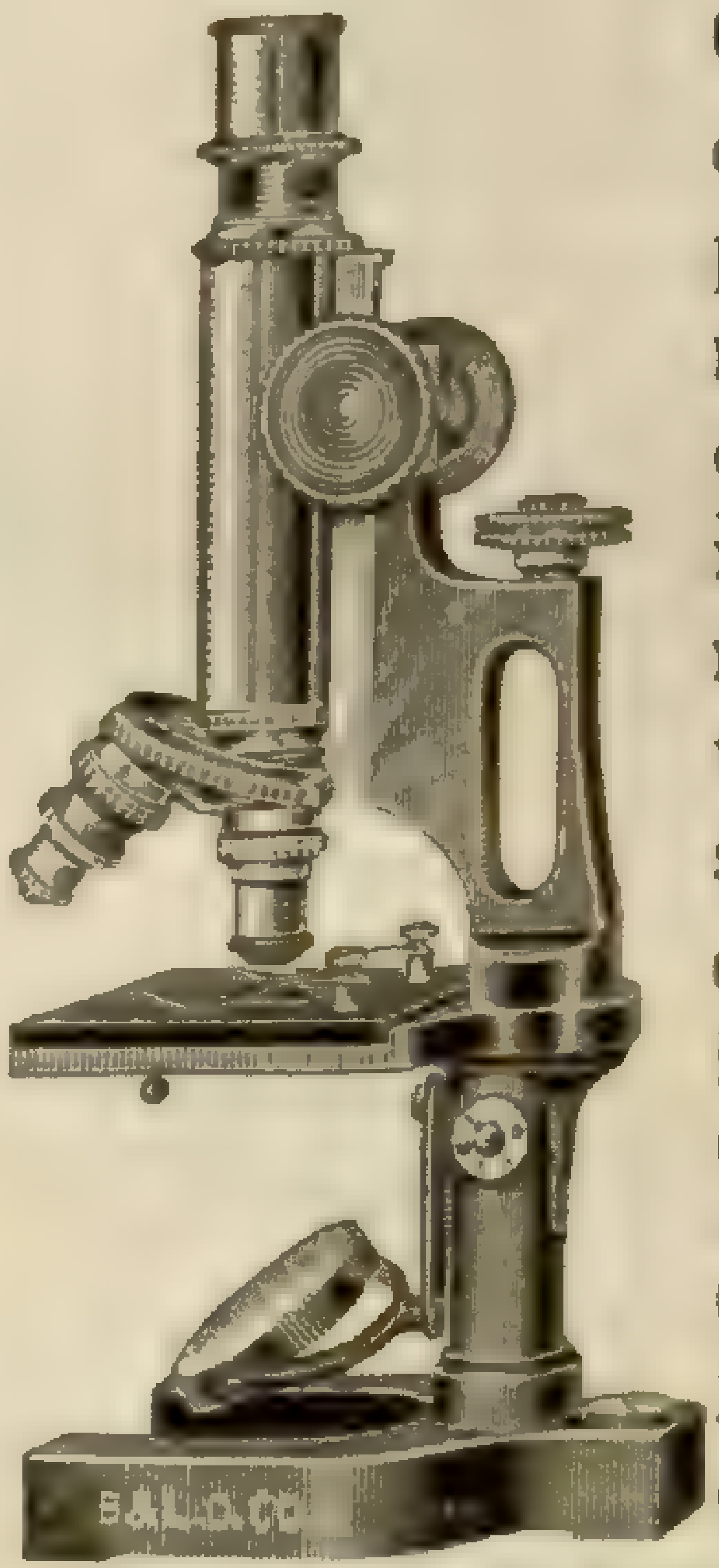

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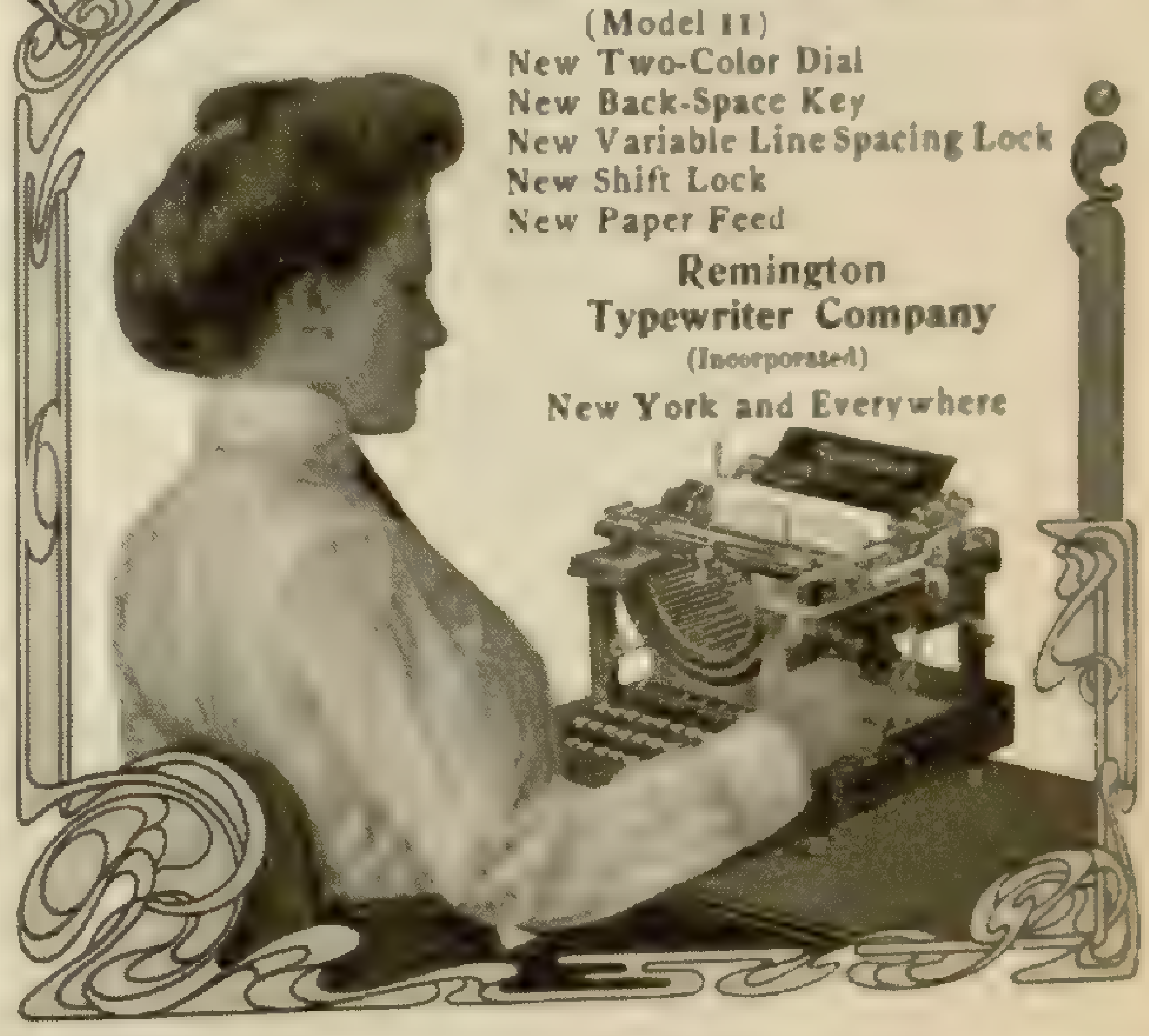

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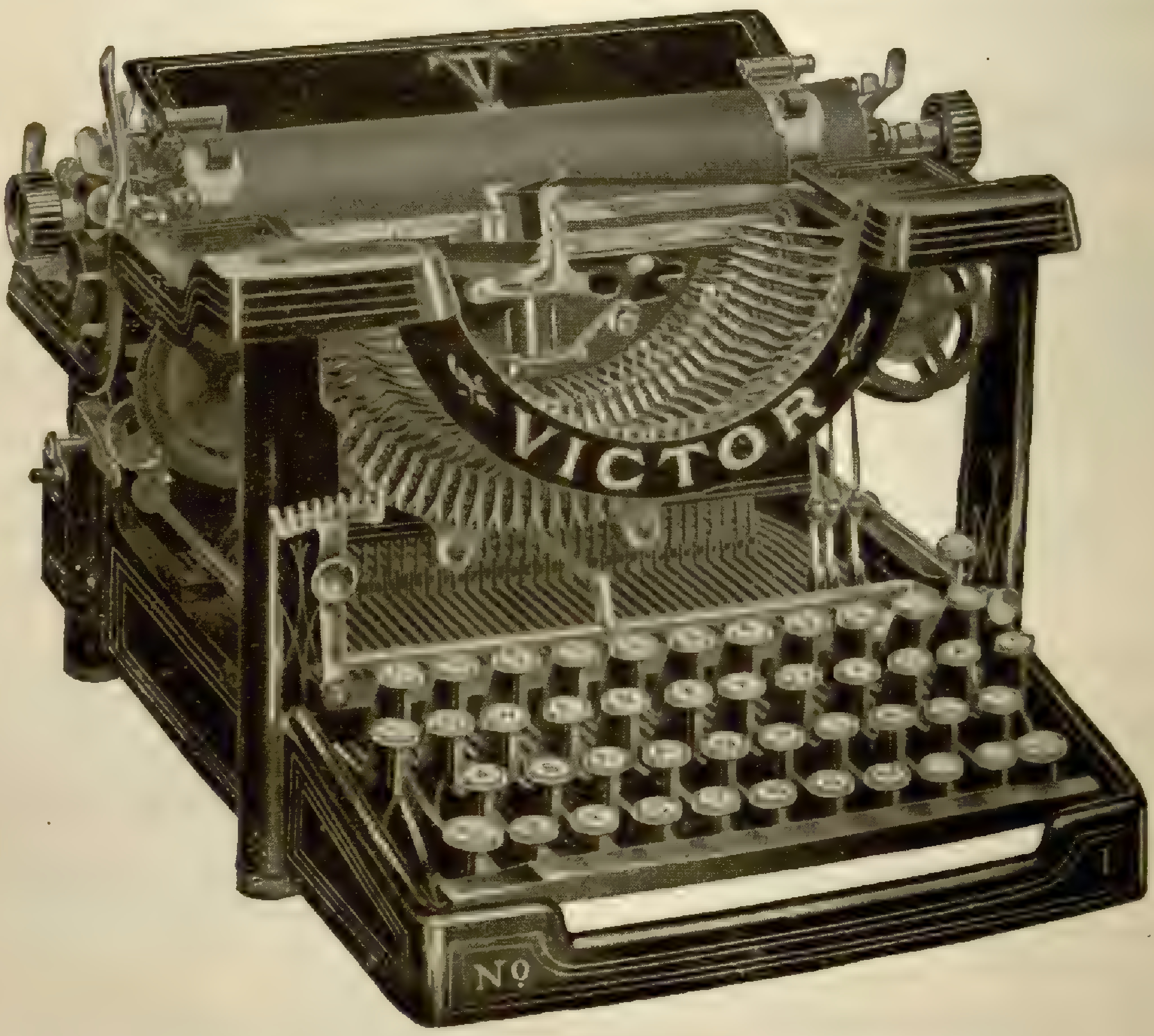

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*) Belgien: 187, Deutsches Reich: 2129, Frankreich: 2078, Groß-Britannien: 1184, Italien: 469, Niederlande: 282, Österreich-Ungarn: 987, Rußland: 473, Schweden: 477, Schweiz: 301, Spanien: 137, Britisch Ostindien: 126, Japan: 102, U. S. America (Vereinigte Staaten): 2212, Canada: 152, etc. etc.

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Troisième édition, revue et augmentée.

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BOTANISCHE ZEITSCHRIFTEN.

Periodical Publications of Botany.

Revues Périodiques de Botanique.

Académie Impériale des Sciences de St.-Pétersbourg = **Travaux** du Musée Botanique de l'Académie . . . .

Académie Internationale de Géographie Botanique = **Bulletin** de l'Académie . . . .

Acta Horti Bergiani. Meddelanden fran Kungl. Svenska Vetenskaps-Akademiens Trädgård Bergielund. (Red.: V. B. Wittrock.) — Nordiska Bokhandeln. **Stockholm**, Schweden.

Acta Horti Botanici Universitatis Imperialis Jurjevensis. (Red.: N. J. Kunezow. — Jährlich 4 Hefte. Preis pro Jahrgang M. 7.50 = Fr. 9.—.) — Botanischer Garten, **Jurjew**, Livland, Rußland.

Acta Horti Petropolitani. (Red.: W. Lipsky. — Jährlich 3 bis 4 zwanglos erscheinende Hefte = 1 oder 2 Bände.) — Kaiserl. Botanischer Garten. **St. Petersburg**, Rußland.

Allgemeine Botanische Zeitschrift für Systematik, Floristik, Pflanzengeographie etc. (Herausg.: A. Kneucker. — Jährlich 12 Hefte. Preis pro Jahrgang M. 6.—.) — J. J. Reiff, **Karlsruhe**, Deutsches Reich.

Allgemeine Botanische Zeitung — **Flora.**

Alpenpflanzen = **Berichte** des Vereines zum Schutze und zur Pflege der Alpenpflanzen.

Amateur de Champignons = **L'Amateur** de Champignons.

American Botanist = **The** American Botanist.

Angewandte Botanik = 1.) **Bulletin** des Bureau für angewandte Botanik. — 2.) **Jahresbericht** der Vereinigung für angewandte Botanik.

Annales de la Société Botanique de Lyon. (Paraissant tous le trois mois.) — Georg, Libraire. 36, passage de l'Hôtel-Dieu. **Lyon**, Rhône, France.

Annales des Sciences Naturelles. Neuvième série. **Botanique**, comprenant l'anatomie, la physiologie et la classification des végétaux vivants et fossiles. (Dir.: Ph. Van Tieghem. — Les „*Annales*" paraissent par cahiers mensuels. — Prix de l'abonnement: Paris, Fr. 30.—, Départements et étranger, Fr. 32.—.) — G. Masson et Cie., Éditeurs, 120, boulevard St.-Germain. **Paris, VI**, France.

Annales du Jardin Botanique de Buitenzorg [Java]. (Publiées par M. Treub.) — E. J. Brill. **Leide**, Pays-Bas.

Annales du Musée du Congo. — Botanique. (Publiées par ordre du Secrétaire d'État.) — Spineux et Co., 62, Montagne de la Cour. **Bruxelles**, Belgique.

Annales Mycologici editi in notitiam Scientiae Mycologicae Universalis. (Herausg.: H. Sydow. Jährlich 6 Hefte. Preis M. 25.—. pro Jahrgang.) — R. Friedländer & Sohn, Karlstr. 11, **Berlin N.W. 6**, Deutsches Reich.

Annali di Botanica. (Dirett.: R. Pirotta. — Gli „*Annali*" si pubblicano a fascicoli, in tempi non determinati. Il prezzo sarà indicato numero per numero.) — Prof. Dott. R. Pirotta. R. Istituto Botanico, Via Panisperna 89 B. **Roma**, Italia.

Annals of Botany. (Edited by: I. B. Balfour, D. H. Scott, J. B. Farmer and R. Thaxter. — The subscription price of each volume, 4 parts, is 30 s, post free to subscribers in the United Kingdom, and with a charge of 1 s 6 d per annum for postage to subscribers residing abroad.) — Henry Frowde, Amen Corner **London, E. C.**, England.

Zopf, **Wilhelm**, Dr., Geh. Regierungsrat, o. Professor der Botanik an der Kgl. Universität, Direktor des Botanischen Gartens und Instituts derselben, — Gerichtsstraße 8, **Münster**, Westfalen.

Zschacke*, **Hermann**, Mittelschullehrer, — Gröbzigerstraße 19. **Bernburg**, Anhalt. *(Floristik. Moose. Flechten. Samml. Tausch.)*

Zschokke*, **Achilles**, Dr. phil., Direktor der Weinbau-Versuchsstation und Schule für Wein- und Obstbau, — **Neustadt a. d. Haardt**, Bayern. *(Physiologie. Anatomie. Angewandte Botanik.)*

Zühlke*, **Paul**, Dr. phil., Oberlehrer am Realgymnasium zu Grunewald. — Joachim Friedrichstraße 13, **Halensee** bei **Berlin**. *(Anatomie. Physiologie.)*

Zwiesele, **Heinrich**, Dr. phil., — Kgl. Zentralstelle für Gewerbe und Handel, **Stuttgart**, Württemberg. *(Biologie u. Systematik der Phanerogamen. Samml.)*

BERLIN.

Kgl. Botanischer Garten und Kgl. Botanisches Museum. (Dir.: A. Engler. — Publ.: *„Notizblatt"*.) — Königin Luisestraße 6/8. **Dahlem-Steglitz bei Berlin.**

Botanisches Institut der Kgl. Friedrich-Wilhelms-Universität. (Gegr.: 1820. — Dir.: S. Schwendener.) — Dorotheenstraße 5. **N.W. 7.**

Pflanzenphysiologisches Institut der Kgl. Friedrich-Wilhelms-Universität und Botanisches Institut der Kgl. Landwirtschaftlichen Hochschule. (Dir.: L. Kny.) — Invalidenstraße 42. **N. 4.**

Museum der Kgl. Landwirtschaftlichen Hochschule. (Vorstand der vegetabilischen Abteilung: L. Wittmack.) — Invalidenstraße 42, **N. 4.**

Institut für Landwirtschaftliches Versuchswesen und Bakteriologie der Kgl. Landwirtschaftlichen Hochschule. (Vorstand: O. Lemmermann.) — Invalidenstraße 42, **N. 4.**

Paläobotanische Abteilung der Kgl. Geologischen Landesanstalt und Paläobotanisches Institut der Kgl. Bergakademie. (Vorstand: H. Potonié.) — Invalidenstraße 44, **N. 4.**

Kaiserl. Biologische Anstalt für Land- und Forstwirtschaft. (Errichtet 1905. — Dir.: J. Behrens. — Publ.: *„Arbeiten"*. *„Mitteilungen"*. *„Flugblätter"*.) — **Dahlem-Steglitz** bei **Berlin.**

Pflanzenphysiologisches Institut der Kgl. Gärtnerlehranstalt. (Vorstand: G. Höstermann.) — **Dahlem-Steglitz** bei **Berlin.**

Märkisches Provinzial-Museum. (Gegr.: 1874. — Kustos: R. Buchholz.) — Am Köllnischen Park. **S.O. 16.**

Institut für Gärungsgewerbe. (Dir.: M. Delbrück. — Vorstand der biologischen Abt.: P. Lindner. — Vorstand der bakteriolog. Abt.: W. Henneberg.) — Seestraße 4. **N. 65.**

Versuchsanstalt für Getreideverarbeitung. (Leiter der botan.-bakteriolog. Abt., des Versuchskornhauses u. d. Versuchsmühle: J. Buchwald.) — Seestraße 4a. **N. 65.**

Städtische Botanische Abteilung für Wissenschaftliche und Schulzwecke. (Dir.: Mächtig. — Das Institut liefert Pflanzen zur Besprechung für sämtliche Schulen Berlins.) — Humboldhain. **N. 31.**

Kgl. Akademie der Wissenschaften. (Gegr. 1700. — Publ.: *„Sitzungsberichte"*. *„Abhandlungen"*.) — Potsdamerstraße 120, **W. 35.**

Berliner Gesellschaft für Geschichte der Naturwissenschaften und Medizin. (Gegr. 1906. — Publ.: *„Verhandlungen"* in den *„Mitteilungen"*.)

Botanischer Verein der Provinz Brandenburg. (Gegr. 1859. — Publ.: *„Verhandlungen"*.) — Kgl. Botanisches Museum. **Dahlem-Steglitz** bei **Berlin.**

Deutsche Botanische Gesellschaft. (Gegr.: 1882. — Publ.: *„Berichte"*.)

Deutsche Dendrologische Gesellschaft. (Gegr.: 1892. — Publ.: *„Mitteilungen"*.) — **Ludwigsfelde** bei **Berlin.**

Deutsche Gesellschaft für Orchideenkunde. (Gegr.: 1907. — Publ.: *„Orchis"*.) Dorotheenstraße 1. **N.W. 7.**

Deutsche Kakteen-Gesellschaft. (Gegr.: 1892. — Publ.: *„Monatsschrift für Kakteenkunde"*.) — Rothenburgstraße 30. **Steglitz** bei **Berlin.**

Textprobe aus dem „Botaniker-Adreßbuch", III. Auflage.

Viguier, René, Dr. ès sci. nat., Préparateur de botanique au Muséum d'Histoire Naturelle de Paris, — 5 bis, quai de Bercy, **Charenton,** Seine. *(Anatomie Systématique. Paléontologie végétale.)*

Vilmorin*, Maurice-Lévêque de, — 13, quai d'Orsay, **Paris, VII.** *(Collections botaniques d'arbustes. Plantes de Chine et du Thibet.)*

Vilmorin*, Philippe-Lévêque de, Lic. ès sci. nat., — 23, quai d'Orsay, **Paris, VII.** *(Phanérogames. Génétique.)*

Vincent, Philibert, Élève en pharm., — Rue Bourg-Belais, **Parthenay,** Deux-Sèvres.

Vinçon, Étudiant, — 16, rue Jean-Bouchet, **Poitiers,** Vienne.

Violleau, abbé **Eugène,** Curé-doyen, — **St.-Varent,** Deux-Sèvres. *(Phanérogames. Mousses. Collect. Échanges.)*

Viron, Dr. en méd., Pharmacien en chef de l'Hospice de la Salpêtrière, — 47, boulevard de l'Hôpital, **Paris, XIII.**

Vitou*, Et., — 1, rue Marie-Caizergues, **Montpellier,** Hérault. *(Cécidies. Maladies physiologiques des végétaux.)*

Viviand-Morel*, Joseph-Victor, Rédacteur en chef du „Lyon-Horticole“. — 33, cours Lafayette prolongé, **Villeurbanne,** Rhône. *(Botanique systématique. Phanérogames. Collect. de plantes vivantes.)*

Voirin, Georges, Dr. en méd., — 14, rue Rousseau, **Bar-le-Duc,** Meuse. *(Collect.)*

Vouaux, abbé, Professeur au Collège de la Malgrange, — **Jarville,** près **Nancy,** Meurthe-et-Moselle. *(Mycologie.)*

Vuillemin*, J.-Paul, Dr. en méd., Professeur d'histoire naturelle médicale à la Faculté de Médecine de Nancy, — 16, rue d'Amance, **Malzéville,** Meurthe-et-Moselle. *(Anatomie. Biologie. Systématique. Pathologie. Tératologie.)*

Vuillermoz, Pharmacien, — **Lons-le-Saunier,** Jura. *(Mycologie.)*

Wattiez, R.-P., Professeur, — **Cellule,** par **Riom,** Puy-de-Dôme.

Weiller, Marc, Lieutenant au 21e Régiment d'Artillerie, — Rue de la Font-du-Cro. **Angoulême,** Charente.

Wuitner, E., — 105, rue Victor-Hugo, **Levallois-Perret,** Seine. *(Algues.)*

Ydrac, F.-L., Dr. en pharm., — **Bagnères-de-Bigorre,** Hautes-Pyrénées.

Zeiller*, Charles-René, Membre de l'Institut, Inspecteur général des Mines, Chargé des leçons de paléontologie végétale à l'École Nationale Supérieure des Mines, — 8, rue du Vieux-Colombier, **Paris, VI.** *(Paléobotanique.)*

ABBEVILLE, Somme.

Musées [Musée Communal; Place St.-Pierre. — Musée Boucher de Perthes: Rue B.-de-P.]. (Conservateur: A. Ledieu.)

Société d'Émulation pour l'Encouragement des Lettres, Sciences et Arts. (Fondée en 1797. — Publ.: *„Mémoires“. „Bulletin“.*)

AGEN, Lot-et-Garonne.

Société d'Agriculture, Sciences et Arts. (Fondée en 1776. — Publ.: *„Recueil des Travaux“. „Revue de l'Agenais“.*)

AIGOUAL, [Mont-], Gard (et Lozère).

Jardins Botaniques de l'Aigoual. — 1) Jardin du Pic-de-la-Fajeole. 1500 m. — 2) Jardin à la Molière-du-Trévezel. — 3) Jardin dans la combe de l'Hort-de-Dieu. (Fondés en 1903. — Dir.: Ch. Flahault.)

AIX, Bouches-du-Rhône.

Académie des Sciences, Agriculture, Arts et Belles-Lettres. (Fondée en 1765. — Publ.: *„Mémoires“.*)

AJACCIO, Corse.

Musées. (Conservateur: J. F. Peraldi.) — Collège Fesch.

ALBI, Tarn.

Musée d'Albi. — au Parc de Rochegude.

Société des Sciences, Arts et Belles-Lettres. (Fondée en 1877.)

ALENÇON, Orne.

Musée Scientifique, Archéologique et d'Histoire Naturelle. (Conservateurs: E. Richard et L. Brioux.) — Hôtel de Ville.

Spécimen du texte de la 3e édition de l'„Annuaire des Botanistes“.

Stabler*, **George**, — Levens. **Milnthorpe,** Westmorland, E. *(Mosses. Hepaticae.)*

Stanley, **William**, — 93, Upper Brooke Street, **Manchester,** E. *(Mosses.)*

Stansfield, **Frederic Wilson,** M. D., Physician and Surgeon. — 120, Oxford Road, Reading, Berks, E. *(Biology. Phanerogams. Ferns.)*

Stapf*, **Otto,** Ph. D., F. R. S., F. L. S., F. R. H. S., Corr. M. Deutsche Bot. Gesellsch., Secretary of the Linnean Society, Keeper of the Herbarium and Library, Royal Botanic Gardens, Kew, — Royal Botanic Gardens, **Kew,** near **London.** *(Gramineae. Taxonomy. Phytogeography.)*

Stedman, **C. F.,** — 76, High Street, **Ashford,** Kent, E. *(Phanerogams.)*

Steele*, **A. B.,** — 16, London Street, **Edinburgh,** S. *(Cryptogams.)*

Steet, **Charles,** — Savings Bank Department, G. P. O., **London, E. C.** *(Fungi.)*

Step*, **Edward,** F. L. S., — Oakwood House, Barnett Wood Lane, **Ashtead,** Surrey, E. *(Phanerogams. Ferns. Fungi.)*

Stevens, Mrs. **E.,** — Endicott. **Worcester Park,** Surrey, E. *(Flora of Surrey.)*

Stevenson, **A. P.,** — 10, New Inn Entry, **Dundee,** S. *(Phanerogams.)*

Stewart, **Archibald,** — 6, Hamilton Street, **Partick,** Lanark, S. *(Cryptogams.)*

Stewart, **Samuel Alexander,** A. L. S., — The Museum, College Square, **Belfast,** Co. Antrim, I. *(Phanerogams. Mosses. Collect. Exchange of Mosses and Hepaticae.)*

Stewart, **William,** Captain. — Shambellie, **Dumfries,** S. *(Cryptogams.)*

Stiles, **M. H.,** F. R. M. S., — 10, Avenue Road, **Doncaster,** York, E. *(Micro-botany.)*

Still, **Arthur L.,** — **Addington,** near **Croydon,** Surrey, E. *(Micro-Algae.)*

Stirling, **Sir James,** M. A., LL. D., — Finchcocks, **Goudhurst,** Kent, E. *(Mosses.)*

Stirton, **James,** M. D., F. L. S., — 5, Newton Terrace, **Glasgow,** S. *(Mosses.)*

Stolterfoth, **Henry,** M. D., M. A., — 1, Grey Friars, **Chester,** E. *(Diatoms. Exchange: Microscopical slides or material.)*

Stone, **Sir Benjamin,** Kt., J. P., F. L. S., F. G. S., F. R. G. S., — The Grange, **Erdington,** Warwick, E. *(Geographical botany.)*

Stone, **Herbert,** F. L. S., — Bracebridge Street, **Birmingham,** Warwick, E. *(Vegetable physiology. Forestry. Desires to exchange specimens of wood or will purchase.)*

Stopes*, Miss **Marie C.,** D. Sc. Lond., Ph. D. Munich, University Lecturer on Botany. — Botanical Dep't., The University, **Manchester,** E. *(Anatomy of fossil plants.)*

EASTBOURNE, Sussex, England.

Eastbourne Natural History Society. (Founded 1867. — Publ.: "*Transactions*".) — Technical Institute.

EDINBURGH, Scotland.

Royal **Scottish Museum.** (Founded 1855. — Dir.: J. J. Dobbie. — Keeper of the Nat. Hist. Dep't: W. E. Clarke.)

Royal **Botanic Garden** [Museum and Herbarium]. (Founded 1670. — Regius Keeper: I. B. Balfour.)

Survey of **British Fresh-Water Lakes.** (Founded 1901. — Dir.: J. Murray. — Botanist: G. West.) — Pullar Trust.

Royal Society of Edinburgh. (Founded 1783. — Publ.: "*Proceedings*". "*Transactions*".) — The Mound, Princess Street.

Royal Scottish Arboricultural Society. (Instituted 1854. — Publ.: "*Transactions*". — 5, St. Andrew Square.

Botanical Society of Edinburgh. (Founded 1836. — Publ.: "*Transactions and Proceedings*".) — 5, St. Andrew Square.

Edinburgh Field Naturalists' and Microscopical Society. (Publ.: "*Transactions*".) — 20, George Street.

Scottish Microscopical Society. (Publ.: "*Proceedings*".) — Philosophical Institution, 4, Queen Street.

Scottish Natural History Society. (Founded 1881. — Publ.: "*Transactions*".) — 5, Queen Street.

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Brizi*, **Ugo**, Dott., Professore di Fisiologia e Patologia vegetale nella R. Scuola Superiore d' Agricoltura e Direttore del Laboratorio di Patologia Vegetale. — Via Marsala, 8, **Milano.** *(Fisiologia. Patologia vegetale. Crittogame.)*

Bruschi*, Signorina **Diana**, Dott. in Sci. nat., — Via del Lavatore, 32, **Roma.** *(Fisiologia.)*

Bruttini, Arturo, Libero Docente di Agronomia. — R. Stazione Agraria. Via S. Susanna, **Roma.**

Buscalioni*, **Luigi**, Dott., Professore ord. di Botanica, Direttore del R. Istituto Botanico dell'Università, — **Catania**, Sicilia. *(Istologia.)*

Cacciamali, Giovanni Battista, Professore di Storia Naturale. — R. Liceo. **Brescia.**

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May 1909

Editors: JOHN M. COULTER and CHARLES R. BARNES

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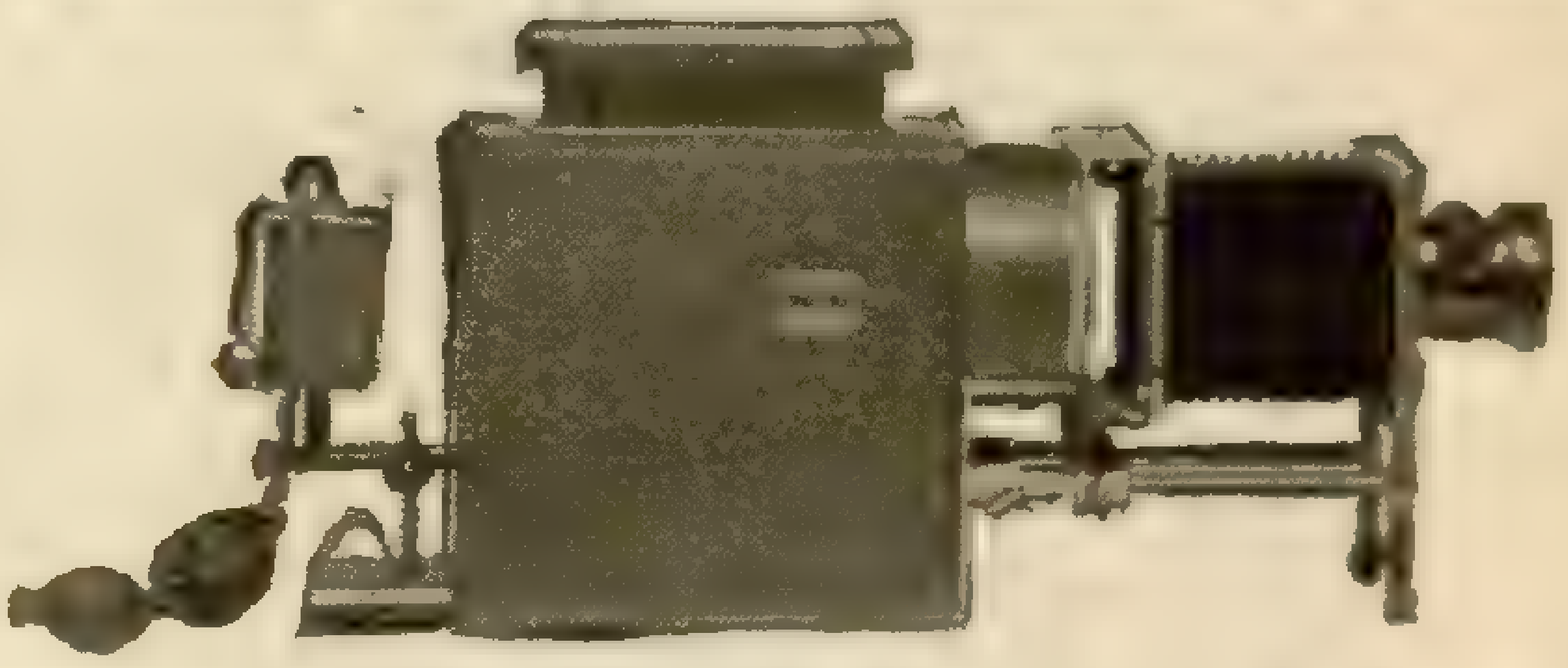

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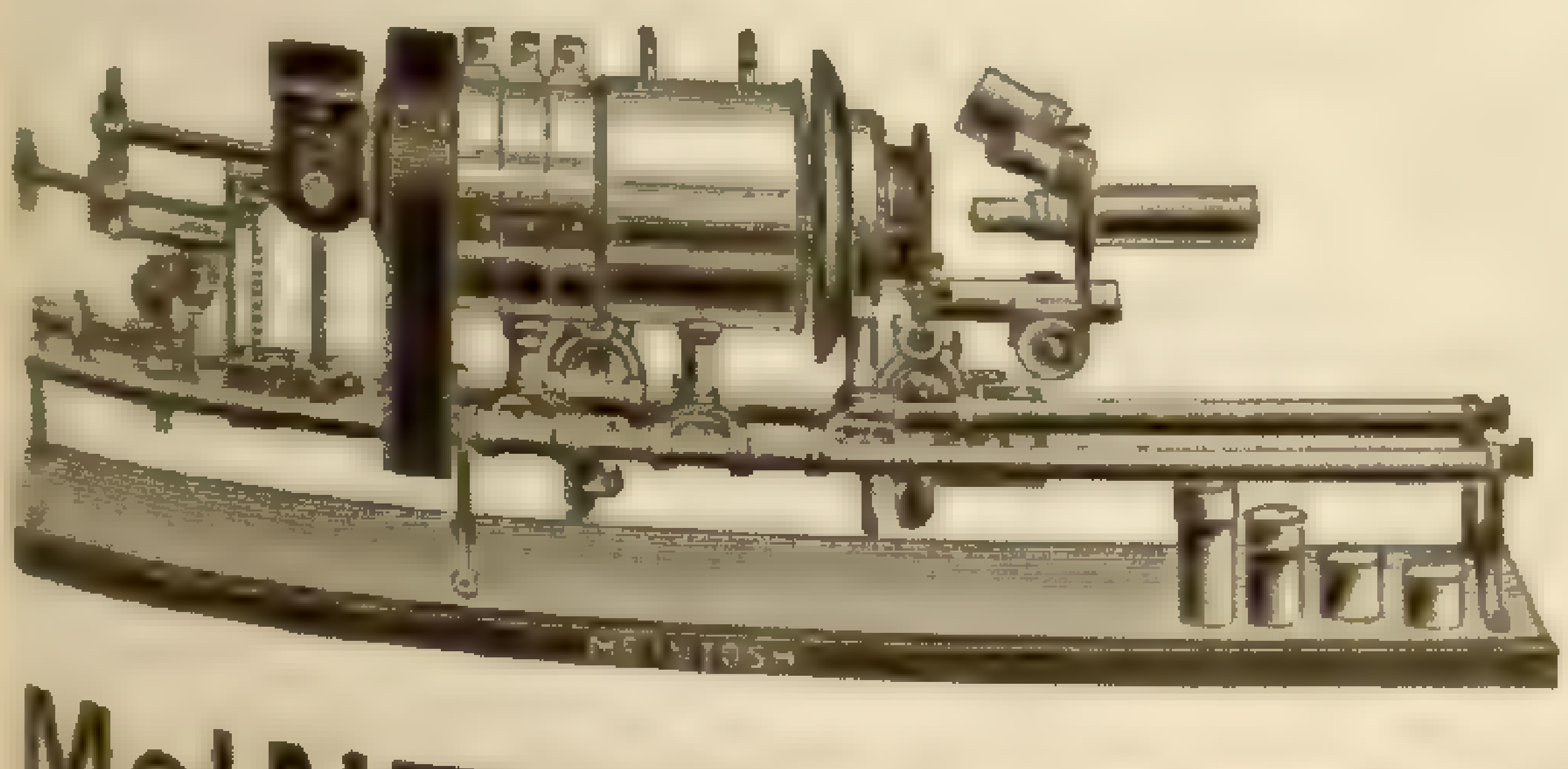

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BOTANICAL GAZETTE

MAY 1909

THE MEGASPOROPHYLL OF SAXEGOTHAEA AND MICROCACHRYS

ROBERT BOYD THOMSON

(WITH PLATES XXII–XXV)

In the Coniferae great importance attaches to "inverse orientation" as a criterion for determining the character of the fertile scale in the megasporangiate cone. The followers of BRAUN see in the inversion of the ovuliferous scale bundles an indication of the "brachyblast" character of this structure. SACHS and EICHLER, the exponents of the "ligular" theory, look upon the inversion as a feature which characterizes the vascularization of a ligule or of an appendage of the simple sporophyll. CELAKOVSKY partly combines the two views and seems to homologize many of the diversified megasporangiate features of the gymnosperms. In the present study some neglected phases of the inversion of the sporangial supply bundles of both the staminate and ovulate cones are given prominence, and data are advanced to show the homology of the micro- and megasporophyll in Saxegothaea and Microcachrys.

The gross features of a fruiting branch of Saxegothaea are indicated in *fig. 1*. The megasporangiate cones are borne terminally on the branches (*figs. 1, 2*), the microsporangiate ordinarily in the axils of foliage leaves, but occasionally in a terminal position (*fig. 3*). The megasporangiate cone, at the stage indicated in *fig. 2*, has a short pedicel beset with the bracts which earlier inclosed it. Later the pedicel elongates and a lax arrangement of the bracts is evident (*fig. 4*). Still later the pedicel becomes much more elongated and relatively very slender. The bracts, sporophylls, and foliage leaves are spirally arranged, and gradations in form are evident, the bracts gradating apically into sporophylls and basally into vegetative leaves (*fig. 4*). The microsporangiate cones may be either sessile or pedicellate. In either case there is a series of spirally arranged bracts closely investing the base of the cone, the lower part of the pedicel, when present, being naked (*figs. 2, 3*). In an otherwise abnormal cone I found the arrangement of bracts similar to that on the megasporangiate pedicel.

The gross features of Microcachrys are indicated in a figure of a previous article.[1] The cones are always terminal in this form and their sporophylls verticillate, in series of fours, the series alternating with one another and presenting from the exterior an appearance of a spiral arrangement (*figs. 5, 6*). The small concrescent foliage leaves are opposite, in alternating pairs.

The form and structure of the microsporophyll of Saxegothaea are indicated in *figs. 7–9*. Two are shown cut longitudinally (*fig. 7*), and between these is one cut through the sporangium, showing the stomium and the wall with its columnar, comparatively thick-walled, epidermal cells. The inner layers of the wall have collapsed, but there are indications of three or four of these.[2] In the axial sections the vascular bundle with its accompanying resin duct is seen, and the connection of these with those of the axis of the cone. The resin canal is expanded distally. This is apparent in the tangential section of the cone as well (*fig. 9*), where the central sporangia often show little trace of a canal, while in the lateral ones it is large. In *fig. 8* resin canals and vascular bundles are seen in transverse sections of the cone, at various distances from the axial supply. In some of the sporangia, to the right of the figure, the position of the stomia is indicated. The microspores contain three cells at the stage from which these figures were made. Megasporangiate cones of the same date have not differentiated the megaspore (*figs. 10, 11*), with the exception of some abnormal ovules, to be described later. A single bundle accompanied by a resin canal passes into each sporophyll, and this gives off the ovular supply just as the point of insertion of the integument is reached

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[1] THOMSON, R. B., On the pollen of Microcachrys. BOT. GAZETTE 47:26–20. *pls. 1, 2.* 1909. See *pl. 1.*

[2] Cf. NORÉN, C. O., Zur Kenntnis der Entwicklung von *Saxegothaea conspicua* Lindl. Svensk. Bot. Tidskr. 2:101–122. *pls. 7–9.* 1908.

fig. 11). *Fig. 12* is a transverse section of the sporophyll a little nearer the cone axis than the point indicated. It shows a single vascular bundle, and below it the accompanying resin duct. The wood (lighter in the figure) is roughly triangular in outline. Near its center are two very darkly nucleate cells. These mark the separation of the wood of the ovular supply from that of the main bundle. The bast above this is but slightly differentiated, and nearer to the axis of the cone dies out completely, as does the wood itself in its further course through the cortex. Under the base of the ovule the bast is quite apparent on the upper side of the supply bundle (*fig. 11*), which shows a tendency to bifurcate, the branches passing laterally into the base of the integument. Beyond the separation of the ovular supply, the main bundle gradually acquires a new set of centripetal wood elements, the more central ones of which are elongated, the lateral quite typical transfusion tissue.

In material of Saxegothaea some six months older than the former, the vascular system of the megasporophyll is further developed. It has been recently described by Miss STILES,[3] with whose account my own observations are practically in accord. The upper vascular system may be composed, in the region of the ovule, of as many as four strands. These, however, in all the material I examined, unite into two before passing upward into the base of the ovule. Miss STILES speaks of there being about three bundles in this region. The pair terminates at the level of the base of the nucellus in a considerable expansion of transfusion-like tissue. The main bundle of the sporophyll is replaced by a series somewhat similar in the same region in which the proliferation of the ovular set occurs. Above the ovule a single bundle is found, with centripetal, and on its flanks a considerable, development of xylem elements. The vascular supply for the scale cones from the axis is a single bundle with normally oriented wood and bast. In the cortex gradually new xylem elements are formed opposite the protoxylem. Farther out wood and bast coming off the sides of the main bundle supplement the original central elements, which up to this point appear not to have any bast of their own. In the further course the proliferation of the upper and lower series occurs, as described above. All of the upper series of bundles pass into the base of the ovule, the only xylem elements found beyond the ovule in this region being a new development associated with the main bundle. A single resin duct accompanies the latter throughout its course. This does not branch and is the only representative of the tissue in the scale, no canals being formed in connection with the upper series of bundles.[4]

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[3] STILES, W., The anatomy of *Saxegothaea conspicua* Lindl. New Phytol. 7: 209–222. 1908.

The vascular system of the axis of the megasporangiate cone consists of a ring of collateral bundles very similar in general to that of the microsporangiate cone (*fig. 8*). The wood of these is usually of the ordinary endarch type, but near the base of the cone there are often a few centripetal elements associated with the bundles at the sides of the gap left by the exit of the megasporophyll trace. In one instance these were almost in continuity with the wood elements of the ovular supply in the sporophyll. The latter, especially in its young condition, appears very much of the nature of centripetal xylem (*fig. 12*),[5] and the occurrence of the isolated elements in the axis affords confirmation of this idea. They are found also in the upper part of the pedicel, but in my material they are rare here.

The scales at the base of the micro- and megasporangiate cones and the foliage leaves both receive a single vascular bundle and a single resin duct from the axis, the supply coming off in a similar way to that of the sporophylls. There is always a gap in the cylindrical stele opposite the "trace" to each of these members (*fig. 8*, for microsporophylls, lower right hand side, etc.).

In several of the megasporangiate cones of Saxegothaea a few of the lower sporophylls bear ovules on their under surface (*fig. 10*). These have an integument, but not the epimatium or rudimentary second integument of the normal ovule. They stand out too from the sporophyll more freely, and are further developed than the upper ones in the same cone. A slight vascular supply goes off to some of these, the bast and wood showing a tendency to orient itself inversely to that of the main bundle of the scale. This supply passes around the resin duct.

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[4] Cf. STILES, *l. c.* 216.

[5] Miss STILES has come to a similar conclusion from studying the more mature condition.

In Microcachrys a single vascular bundle supplies leaf and sporophyll. There are no resin canals in the stem nor in the axis of either cone. It is not until well out into the sporophyll that a canal is found beneath the vascular bundle (megasporophyll, *fig. 13*). The canal of the vegetative leaf, however, is continued downward into its swollen base, and the leaves being concrescent, there is the appearance of resin ducts in the stem. The vascular bundle in both leaf and sporophyll runs closer to the upper than the lower surface. A comparison of longitudinal sections of the megasporophyll and vegetative leaf shows a great resemblance between the distal part of the former and the whole of the latter. There is a distinct palisade on the lower surface of each, a sclerotic hypoderma, and an epidermis with a very thick cuticle and no stomata, the latter being restricted to the upper surface, and in the case of the sporophyll, so far as I have observed, to the region beyond the ovule. There is no hypoderma on the upper surface, and the same kind of degenerate-looking palisade tissue occurs in both sporophyll and leaf. Proximally the sporophyll is contracted into a slender stalk, while the leaf is concrescent with the stem. The vascular supply of the ovule originates in much the same way as in Saxegothaea with at first no apparent bast[6] (*fig. 14*; above the resin canal come bast and wood of the main bundle and above the center of the latter the few wood elements of the ovular supply). On separation the ovular supply bundle passes obliquely upward, as in Saxegothaea (cf. *figs. 11* and *13*), with bast clearly evident on its upper side. In Microcachrys, the single supply bundle bifurcates near the base of the ovule, the divisions passing well into the basal part of the integument.

In most of my material the megaspore of the ovules has only a few nuclei in a parietal stratum of protoplasm (*fig. 13*). In one case, however, a prothallial tissue (*fig. 15*) is present with the archegonial initials discernible. These are located at considerable distances from one another. Around the prothallium the megaspore-coat is of the usual double type.[7] It is slightly thicker than in *Pinus resinosa* at a similar stage. Like the pine coat at this young stage, it is of uniform distribution about the prothallium. It would be interesting to know the condition in the mature seed, especially in view of the fact that in certain species of Dacrydium the megaspore coat is very thick at a later stage.

---

[6] Cf. Worsdell, Observations on the vascular system of the female flowers of the Coniferae. Annals of Botany **13**:538. 1899.

[7] Thomson, R. B., The megaspore-membrane of the gymnosperms. Univ. of Toronto Studies, Biol. Ser. **4**:1–64. *pls. 1–5*. 1905.

The integuments of the ovule are seen in their usual form in *fig. 13*. Sometimes the inner one is quite open above the ovule (*fig. 15*), even at an advanced stage. In the case figured it is developed laterally into two large masses, appearing as additional ovules in gross material. In other cases it may be uniformly quite thick (*fig. 16*). The two outer cell layers of the integument are tangentially elongated in the older condition, while the third consists of columnar cells radially placed, many of which in the basal region become lignified and have numerous large pits. They are in connection with the supply bundles of the ovule through transfusion-like extensions of the latter.

Fig. 17 is of a longitudinal section of the bract and scale from the megasporangiate cone of *Tsuga canadensis*. The section passes to one side of the axis in the region of the ovule. To the lower right-hand side of the figure the bract is seen fused proximally with the tissues at the base of the scale. The latter shows one large vascular bundle, cut nearly transversely. This has the wood below and the bast above, an arrangement the inverse of that in the bract. From this bundle is given off the ovular supply, which passes obliquely upward into the base of the sporangium. The character of the supply bundle was studied in series of transverse sections. It comes off from one of the lateral bundles of the scale (*fig. 15;* second bundle from the right and left of the figure). Its wood and bast lie at first in a plane at right angles to that of the scale bundles (*fig. 19;* the wood is the small-celled tissue in the center of the figure and the bast is to the left). Shortly the bundle turns completely round, so that its wood lies above and its bast below, the inverse arrangement to that of the scale bundles, which, in turn, is inverse to that of the bract. Near the ovule the bundle becomes concentric and finally bifurcates, the branches entering the base of the integument.

In the microsporophyll of the cycads THIBOUT[8] has called attention to the inverse orientation of the sporangial supply. I have figured that of *Ceratozamia mexicana* (*fig. 21*). In *fig. 21* the upper bundle is one of the normally oriented main bundles—bast below and wood above, not shown in the section—while cutting obliquely across the field is a sporangial supply bundle with bast above and wood below. A short ventral extension to the sporangia turns at right angles at first and then becomes almost inverse. *Figs. 22* and *23* are transverse sections of a sporophyll. In the upper part of the figures are the main bundles, with wood above and bast below. Farther down and toward the ends of the normal series are some inversely oriented bundles. One, to the left, magnified in *fig. 23*, has just divided into a similarly oriented bundle, and from this there is a strand to the sporangium. The latter has a more or less concentric character. In some cases I have found a second inversion on the way to the sporangia.

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[8] THIBOUT, E., Recherches sur l'appareil mâle des gymnospermes. pp. 265. *pls. 16.* Lille. 1896.

The inversion of microsporangial supply bundles is of wide occurrence in the cycads, but is not confined to the group, being also found in certain conifers. This feature has not been considered by the exponents of the theories advanced to explain the inversion in the fertile scale of the latter. That it is of first importance seems self-evident. Again, the double inversion in the fertile scale has not been explained, and a glance at the figures shows how important the second inversion is, both of itself and in comparison with the single inversion in either Saxegothaea or Microcachrys (cf. *figs. 11, 13.* and *17*). This and the occurrence of ovules on the lower surface of the scale in Saxegothaea, and their vascularization from the main supply, would seem to be good reason to consider that inverse orientation cannot in all cases be relied upon as evidence of the brachyblast character of the fertile scale. In the last case, we should have the anomaly of the leaf in the axil of the shoot.

Again, in Dacrydium two bundles with orientation inverse to that of the scale supply the ovule. These attach directly to the axis, the three passing close together near the upper surface of the scale. There is, then, in Dacrydium, a form admittedly of a higher type than either Saxegothaea or Microcachrys because of the reduction of the cone, etc., a greater amount of inversion than in the more primitive forms—a puzzling feature certainly in view of the brachyblast theory, but possibly finding its explanation in the greater importance of the ovule in this specialized fructification and in the greater advantage which a direct connection with the axial supply affords. This has its beginning in Saxegothaea and Microcachrys, where the two bundles of the ovular supply have asserted their individuality only part way to the axis, the ovular supply in these forms having possibly originated, as has been suggested, as a revival of the centripetal development of the main bundle.

In view of the facts presented, the writer is led to look upon the fertile scale as a simple structure, the homologue of the microsporophyll in both Saxegothaea and Microcachrys, and, *ipso facto*, in the whole of the Taxaceae, if these form a natural alliance, as is commonly held. With this group is to be associated the Araucarieae, whose microsporophylls show an inversion of the sporangial supply bundles of like character to that of the megasporophyll,[9] and which, on other grounds, have been considered[10] as having a simple megasporophyll. This group also has recently been shown to have many features in common with the lower podocarps. Perhaps the most important of these are the method of pollination and the absence of wings on the grains themselves in Saxegothaea and the Araucarieae, the extensive microgametophyte of the two groups, the single inverted ovule, the wide micropyle and projecting nucellus, the nucellus free from the integument to its base—features which bring these forms into intimate association.

The simple-scale groups, the Taxaceae and Araucarieae, have then their micro- and megasporangia on opposite sides of the sporophyll; and since the homosporous forms, from which the conifers were derived, the pteropsid series, as is shown on morphological and anatomical grounds, have the sporangia usually on the lower surface, the ovule has probably been transferred to the upper surface in the course of phylogeny. The ovules on the lower surface of some scales of Saxegothaea and their lateral position in Cycas are significant in this connection, and, as well, the lateral development of the sporangium in Schizaeaceae.

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[9] THOMSON, R. B., The origin of the gymnosperms at the Linnean Society. New Phytol. **5**:145. 1906.

[10] SEWARD, A. C., AND FORD, S. O., The Araucarieae, recent and extinct. Phil. Trans. Roy. Soc. London B. **198**:305–411. *pls. 23, 24.* 1906.

COULTER and CHAMBERLAIN, after reviewing the different theories of the fertile scale in their textbook on the gymnosperms, make the following statement (p. 77): "Upon sifting the testimony certain things seem to be fairly clear, and one is that the scale and its ovules in Abieteae represent a highly modified axillary shoot, corresponding to the characteristic spur shoot of the group." From anatomical and teratological evidence this conclusion seems inevitable, and since the Abieteae, Taxodieae, and Cupresseae present such a series of natural affinities the statement must apply to all. If, then, the fertile scale in this group is of the brachyblast type, representing the adaxially fused first and only two leaves of an abortive axis, the first inversion is explained, and the ovules in this group are borne on the morphologically under surface. The second inversion is analagous to the single one in Saxegothaea and of the nature of a sporangial supply. There are, then, two great groups of the conifers from the standpoint of this study, the simple- and the complex-scale series. Both forms have the ovules on the physiologically upper surface, a position rendered almost imperative by the necessities of the seed habit. This position, however, has been attained in two very different, but possibly equally difficult, ways in the aplo- and diplosporophyllous forms of the Coniferae.

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EXPLANATION OF PLATES XXII–XXV

PLATE XXII

FIG. 1.—Fruiting twig of *Saxegothaea conspicua*. Slightly enlarged.

FIGS. 2, 3.—Micro- and megasporangiate cones. ×4.

PLATE XXIII

FIG. 4.—Megasporangiate cone with the axis more elongated than in *fig. 2*.

FIG. 5.—*Microcachrys tetragona;* micro- and megasporangiate cones, the former in mature condition. ×4.

FIG. 6.—Older megasporangiate cone.

FIGS. 7–9.—Respectively radial, transverse, and tangential sections of the microsporangiate cone of Saxegothaea.

FIGS. 10, 11.—Megasporophylls of Saxegothaea, with ovules attached; *fig. 11* showing ovular supply coming off the main vascular bundle.

PLATE XXIV

FIG. 12.—Transverse section of the megasporophyll of Saxegothaea, young condition, just proximal to the insertion of the ovule.

FIG. 13.—Longitudinal section of the distal part of the megasporophyll of Microcachrys.

FIG. 14.—Transverse section of same, showing ovular and main supply bundles in transverse section.

FIG. 15.—Megasporangium of Microcachrys in transverse section.

FIG. 16.—Sporophyll and megasporangium with abnormally thick integument, in transverse section.

FIG. 17.—*Tsuga canadensis;* bract, scale, and ovule in longitudinal section.

PLATE XXV

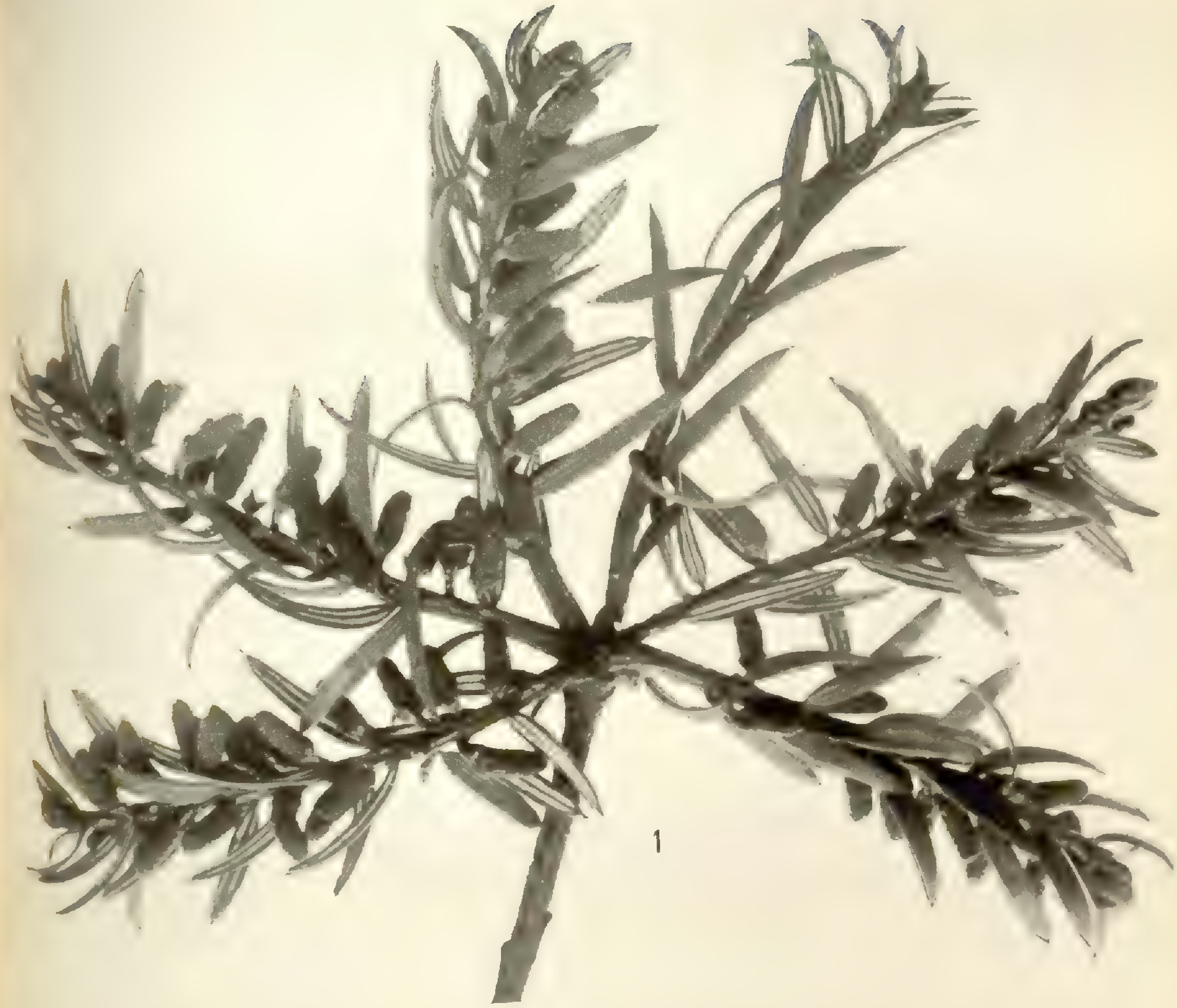
FIG. 18.—*Tsuga canadensis;* transverse section of bract, scale, and ovules at the point of origin of the ovular bundles.

FIG. 19.—The same; a magnification of the ovular supply of the right ovule in *fig. 18.*

FIG. 20.—The same; supply bundle farther up.

FIGS. 21, 22.—Respectively, longitudinal and transverse sections of microsporophyll of *Ceratozamia mexicana.*

FIG. 23.—A magnification of a part of *fig. 22.*



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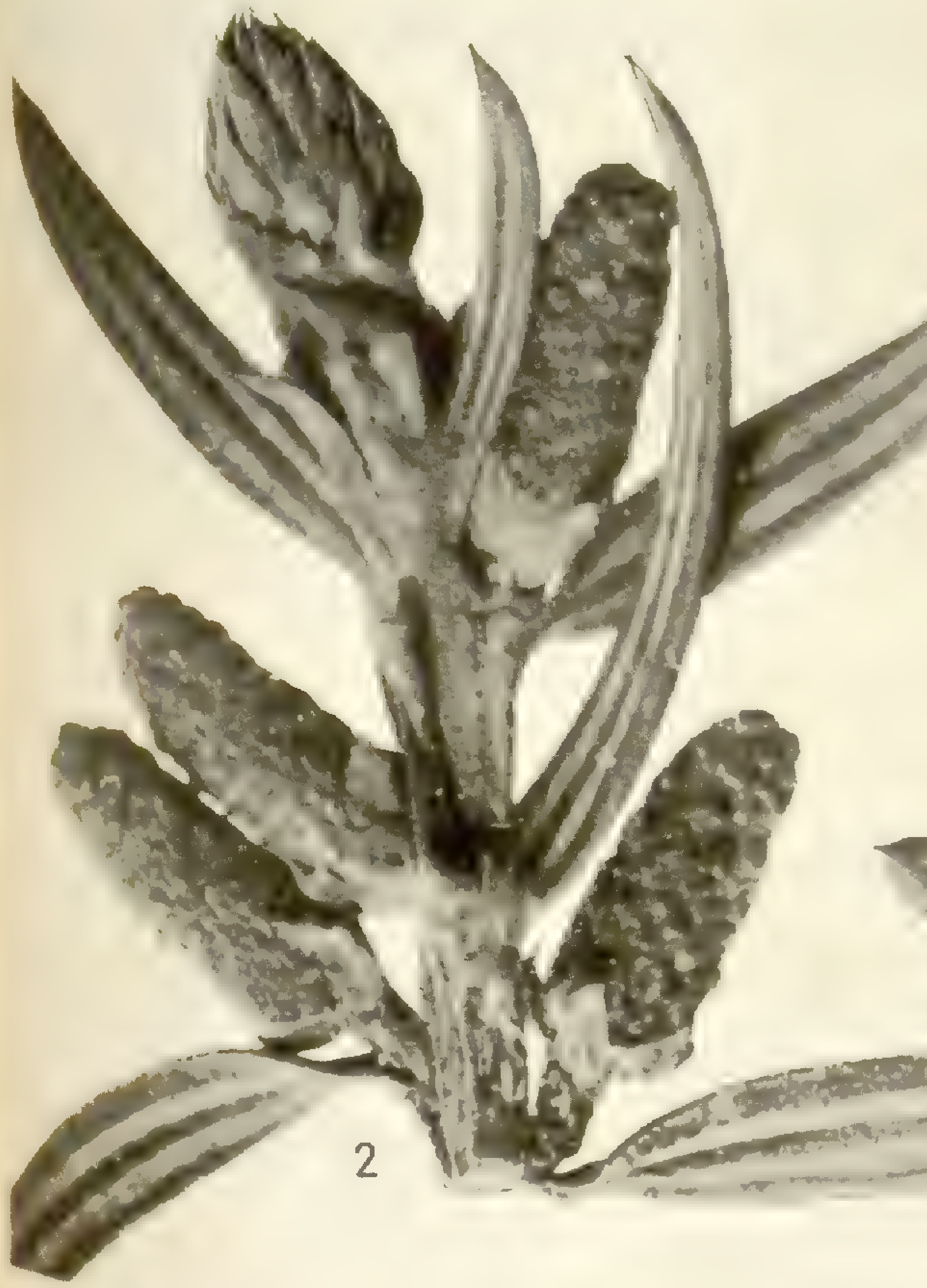

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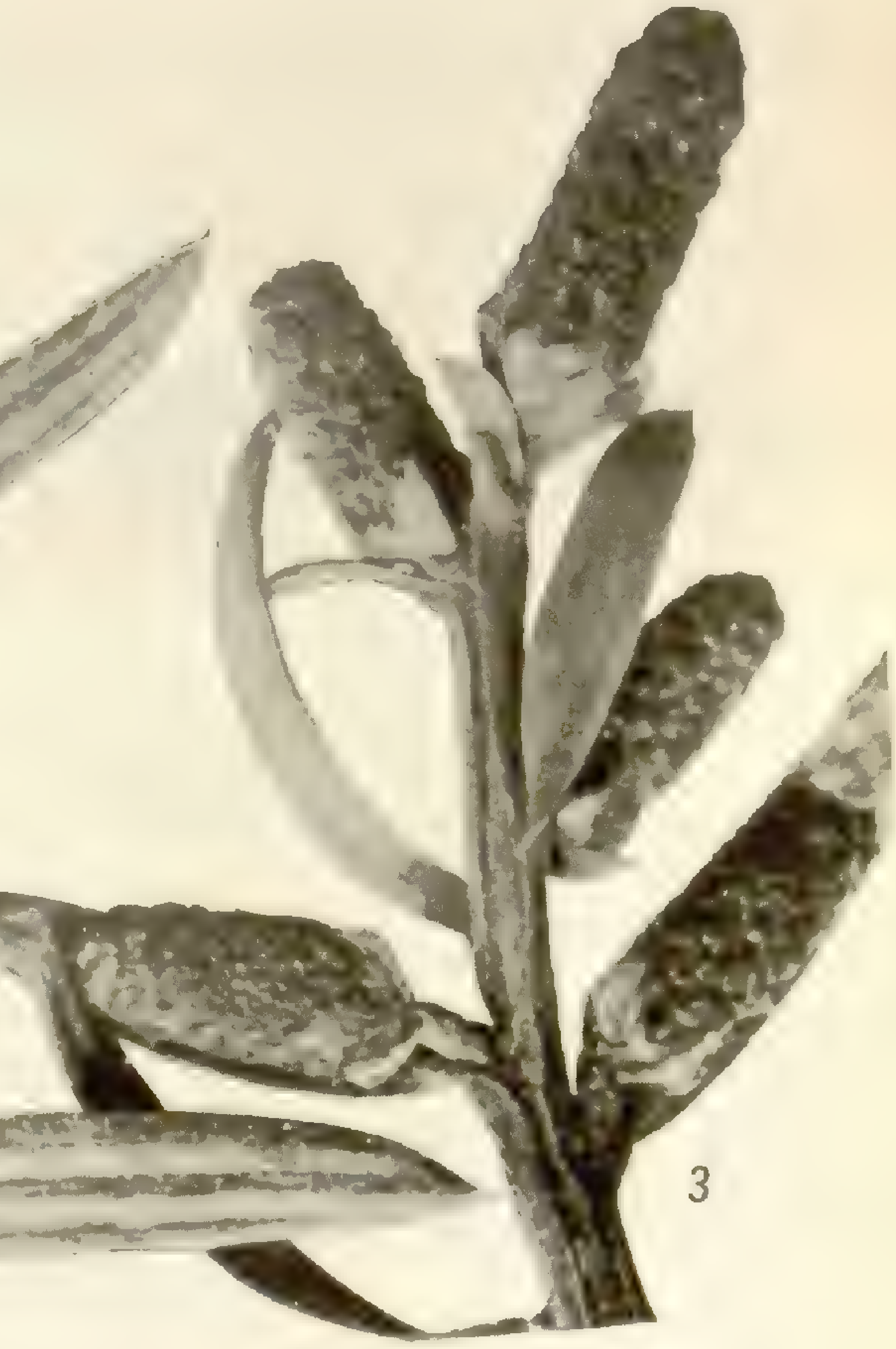

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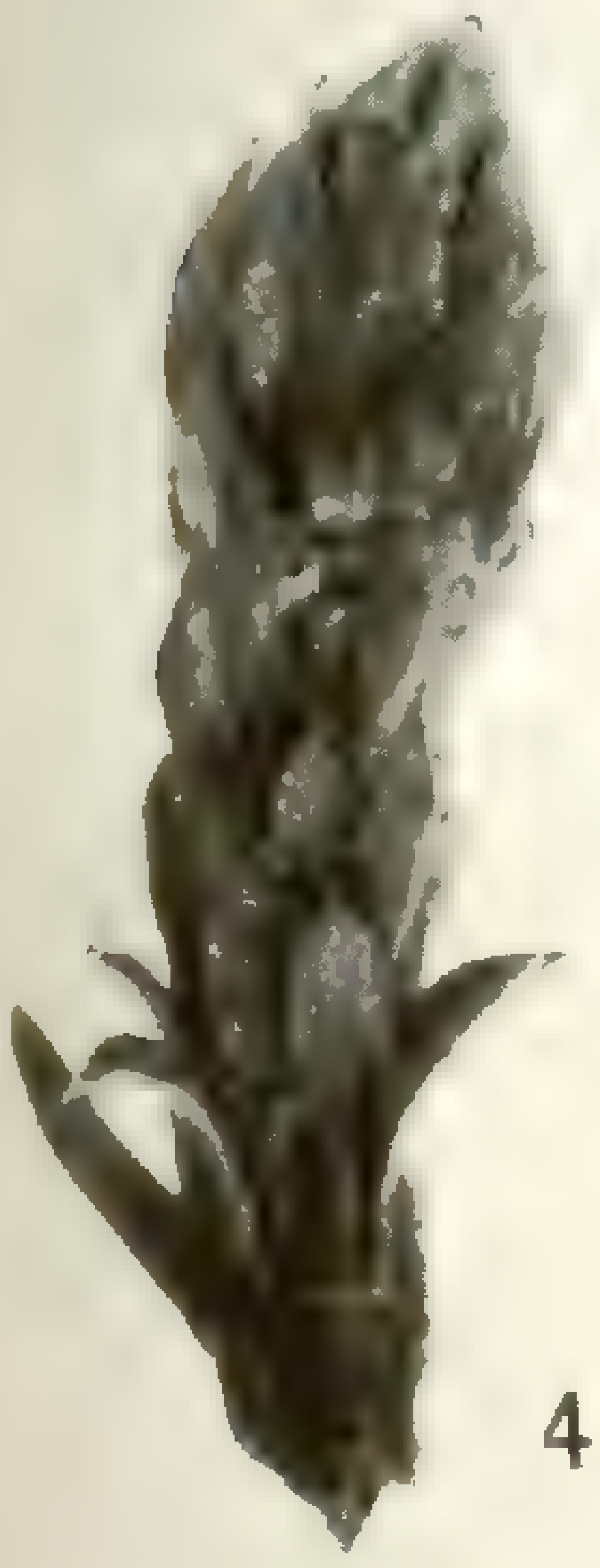
THOMSON on MEGASPOROPHYLL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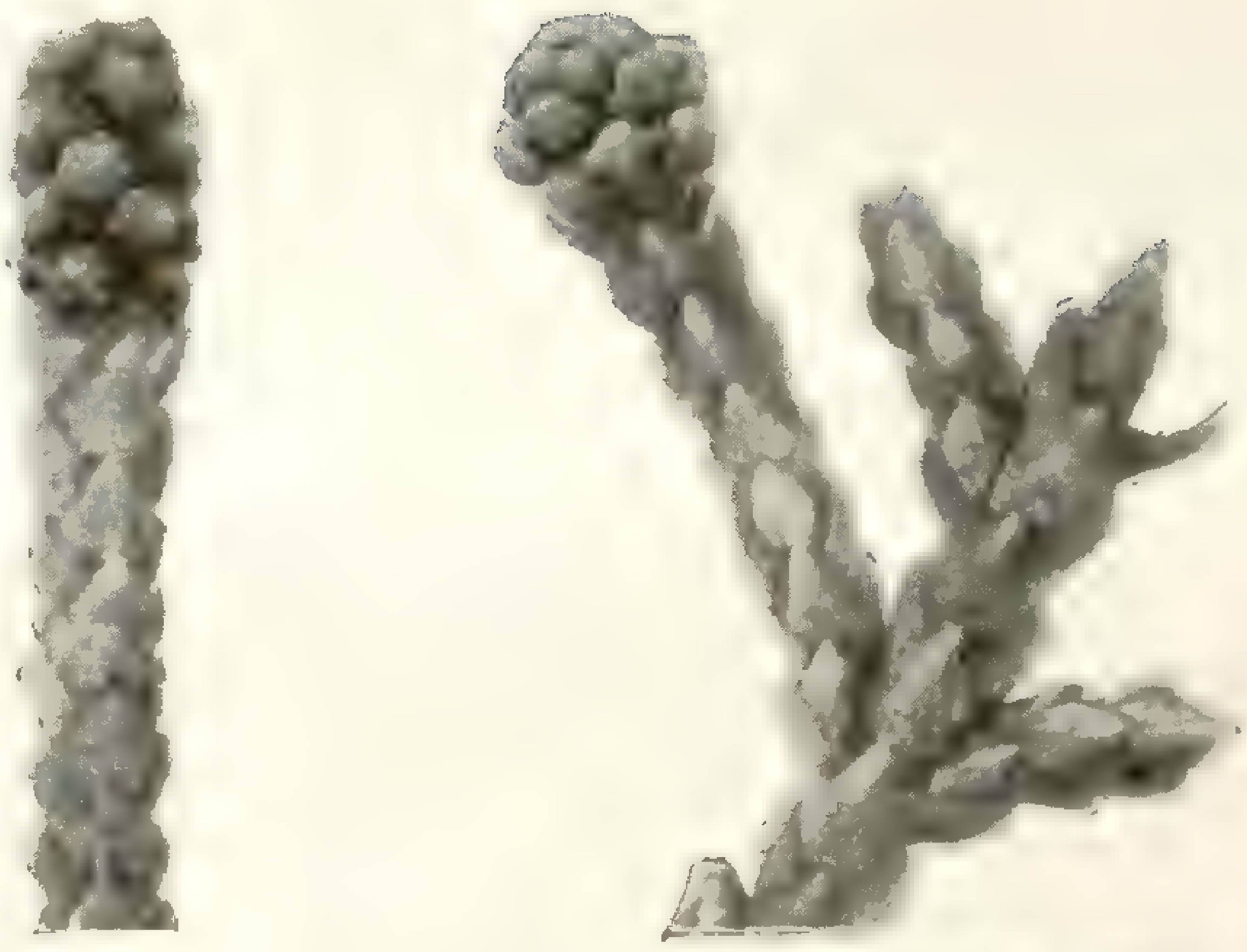
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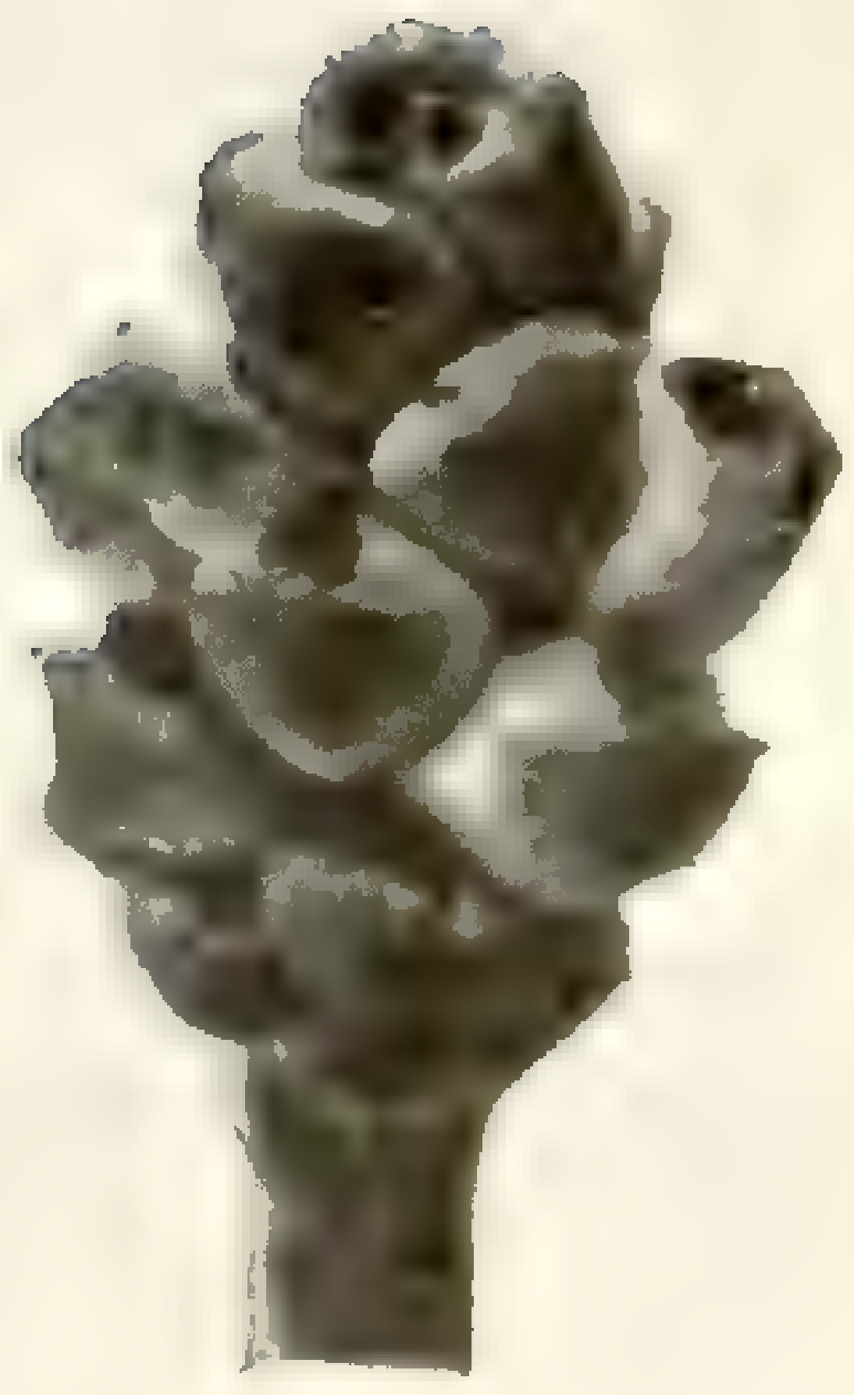
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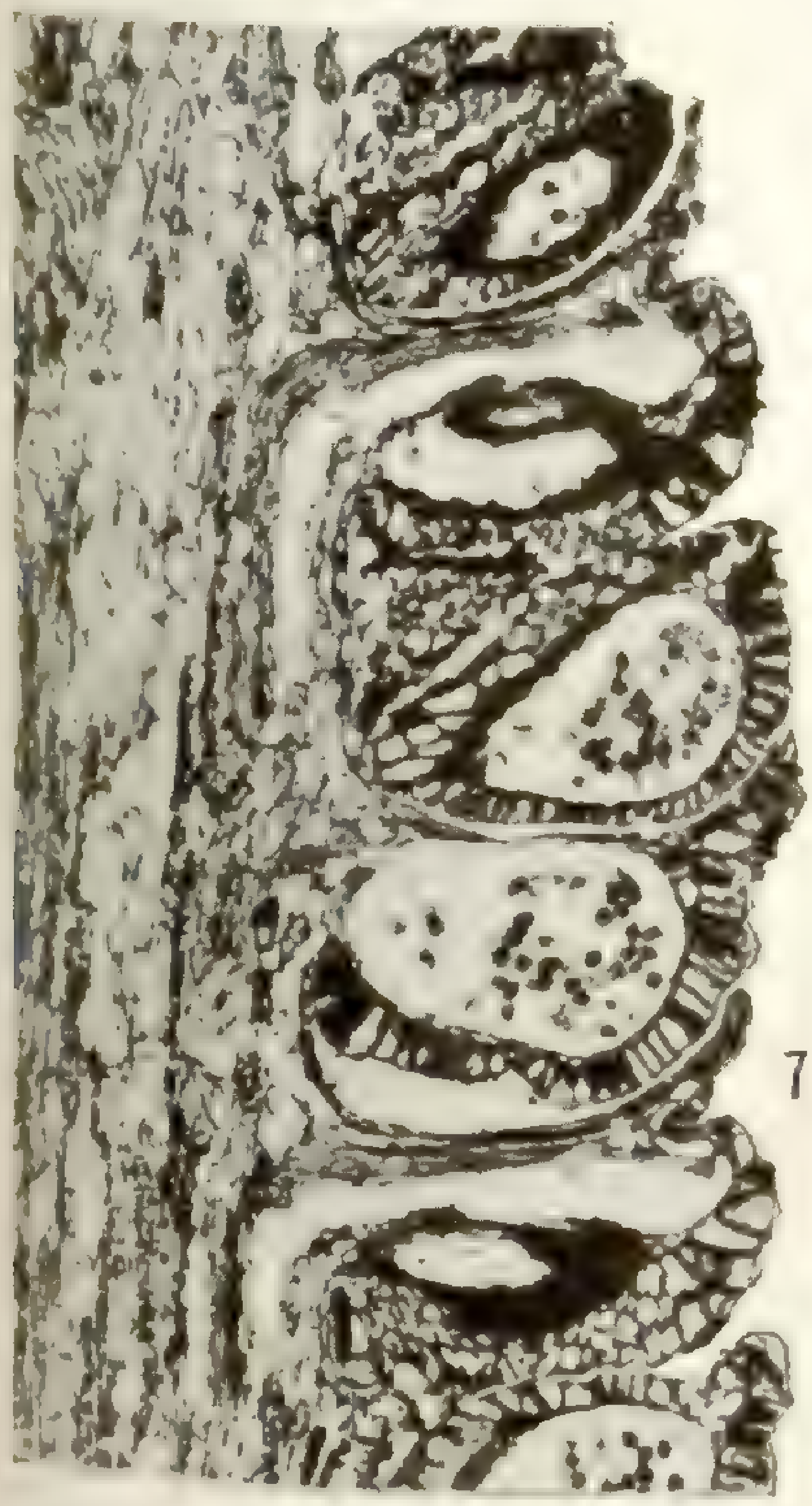
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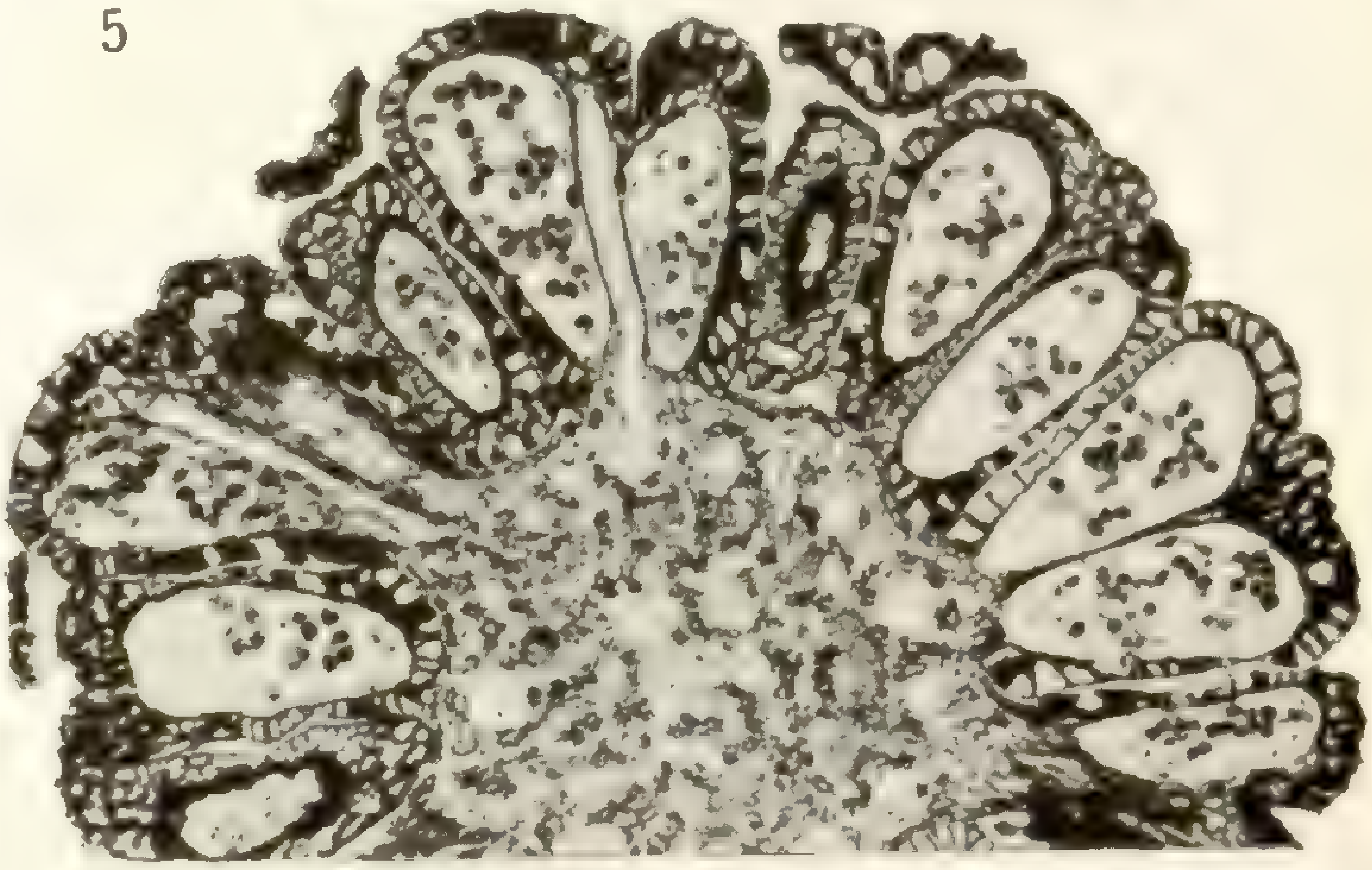
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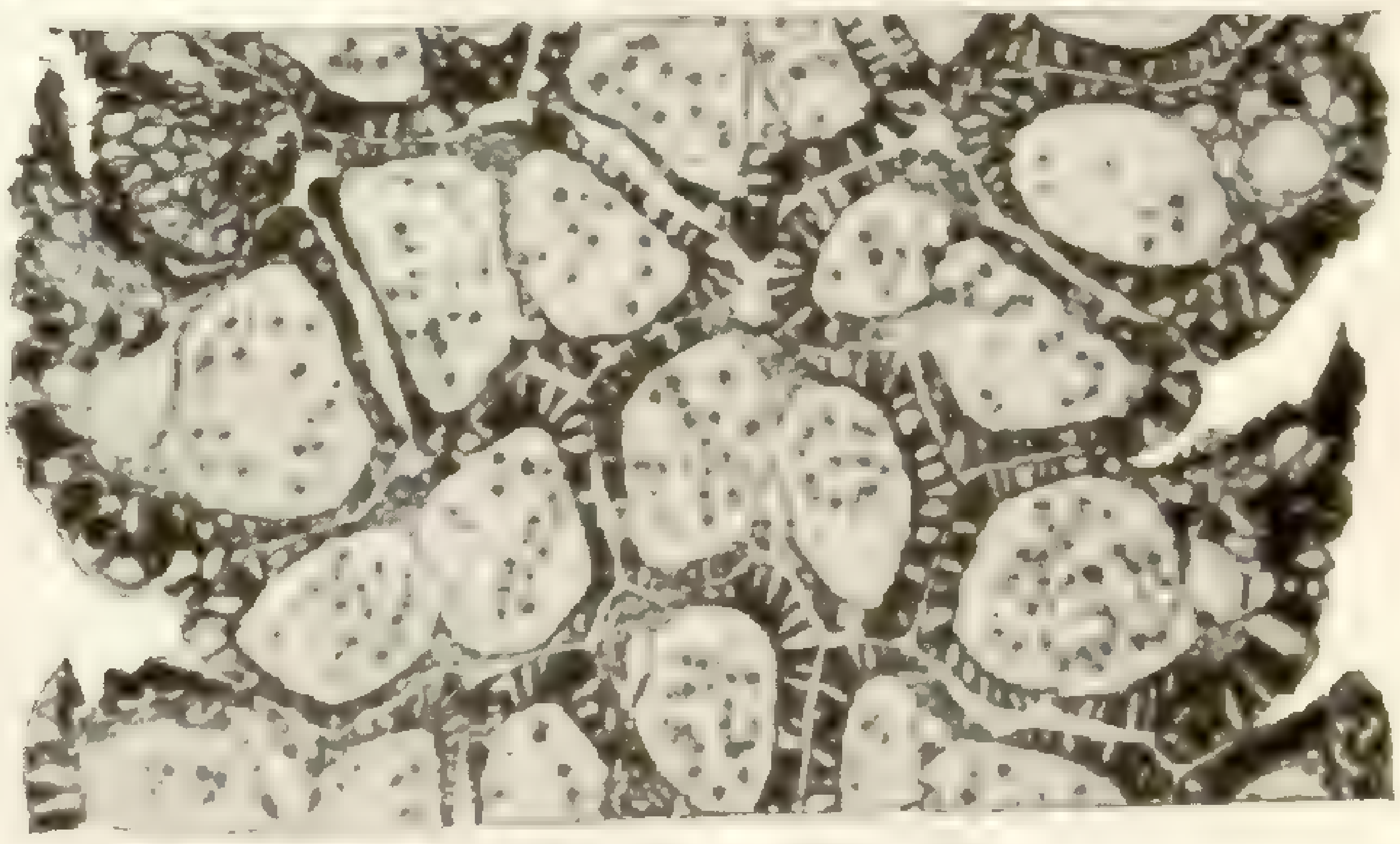
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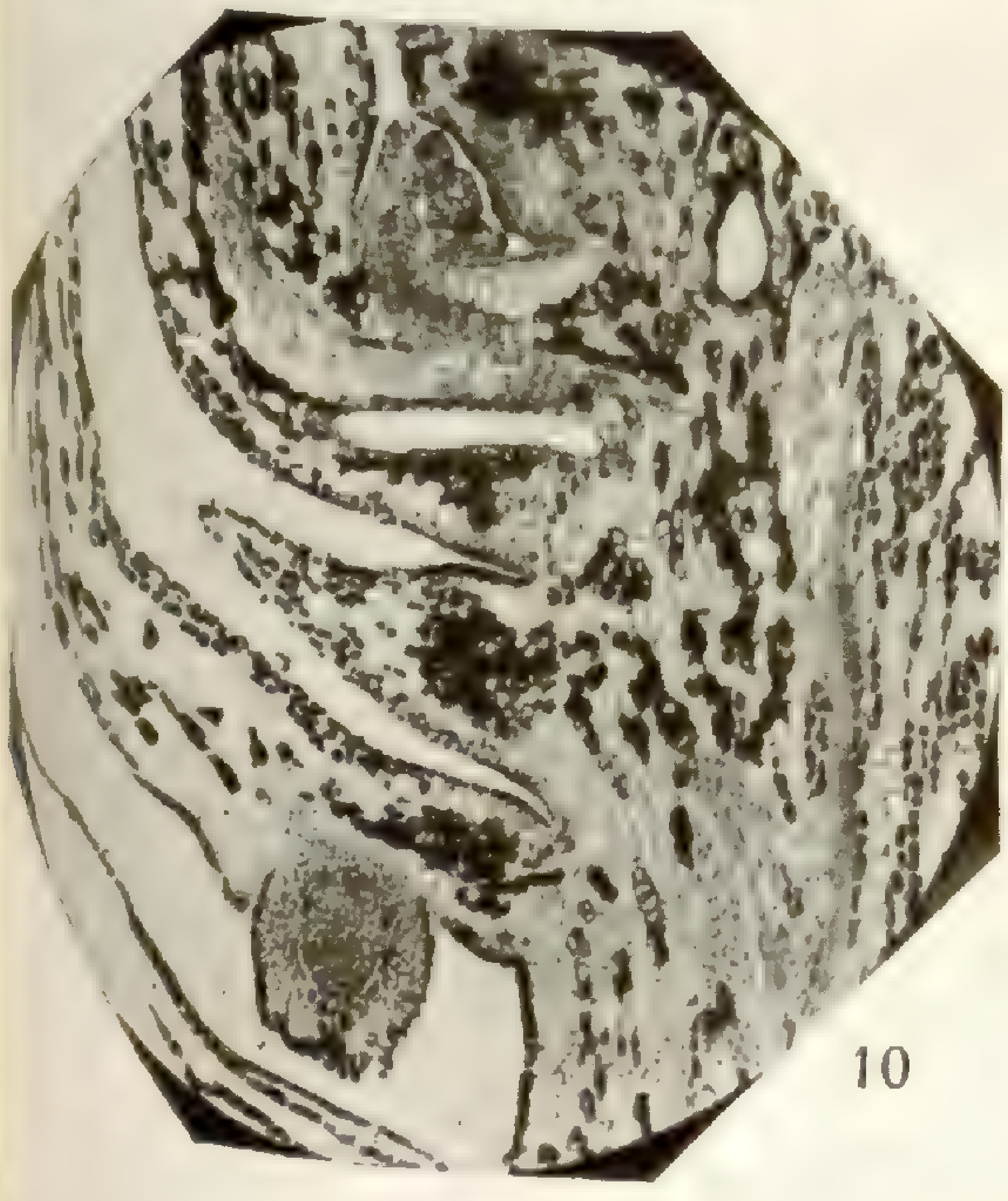
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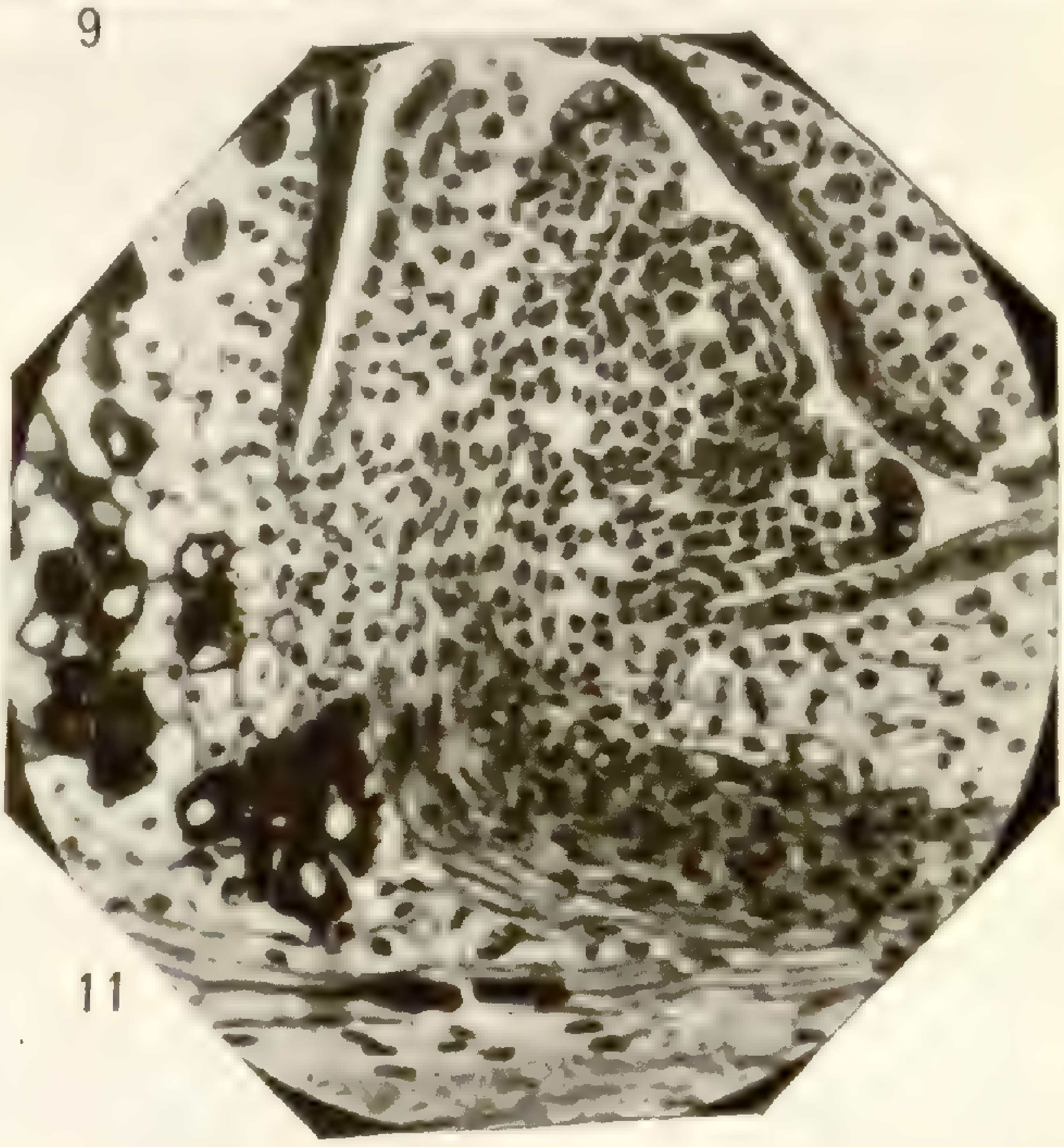
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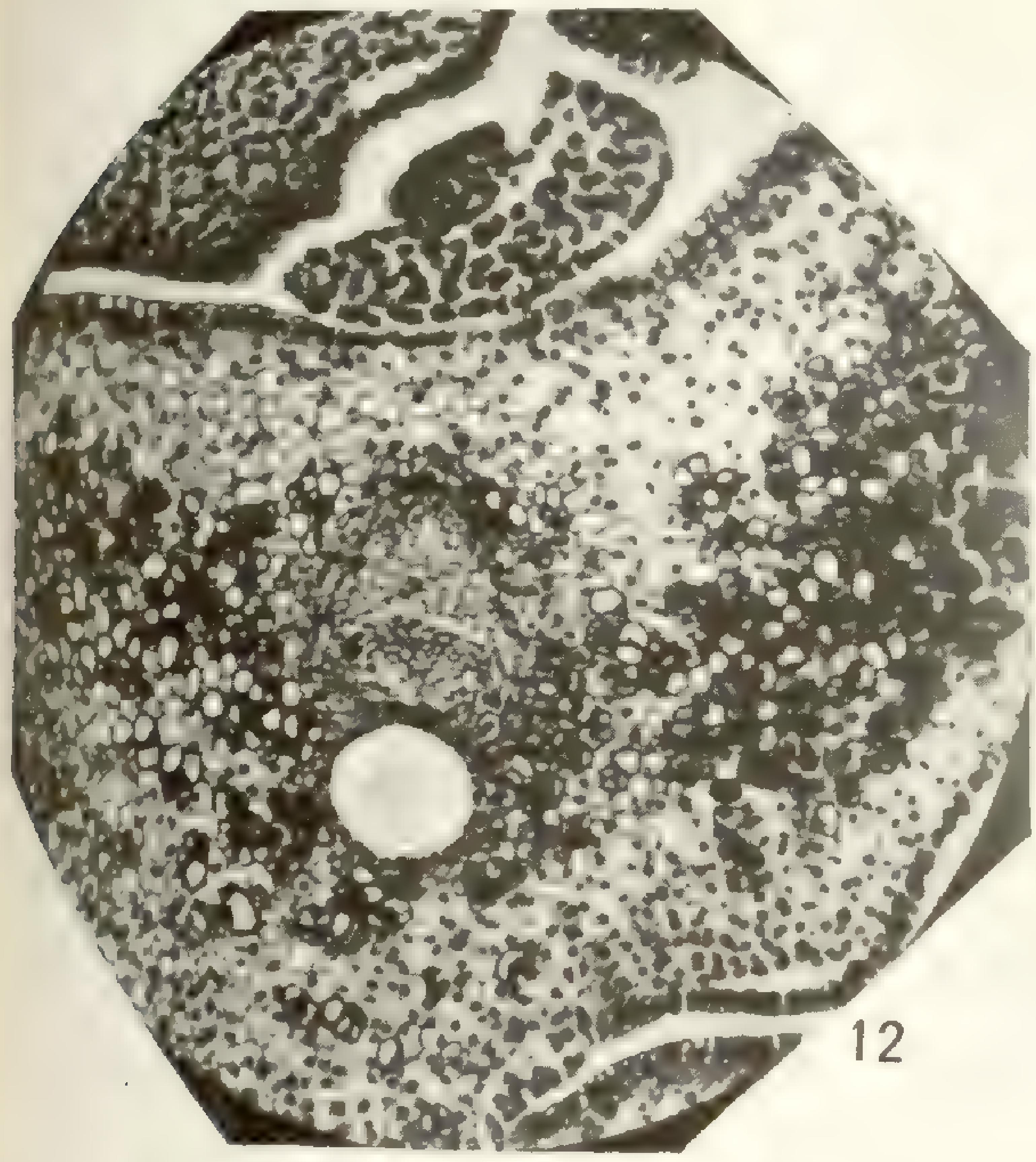
THOMSON on MEGASPOROPHYLL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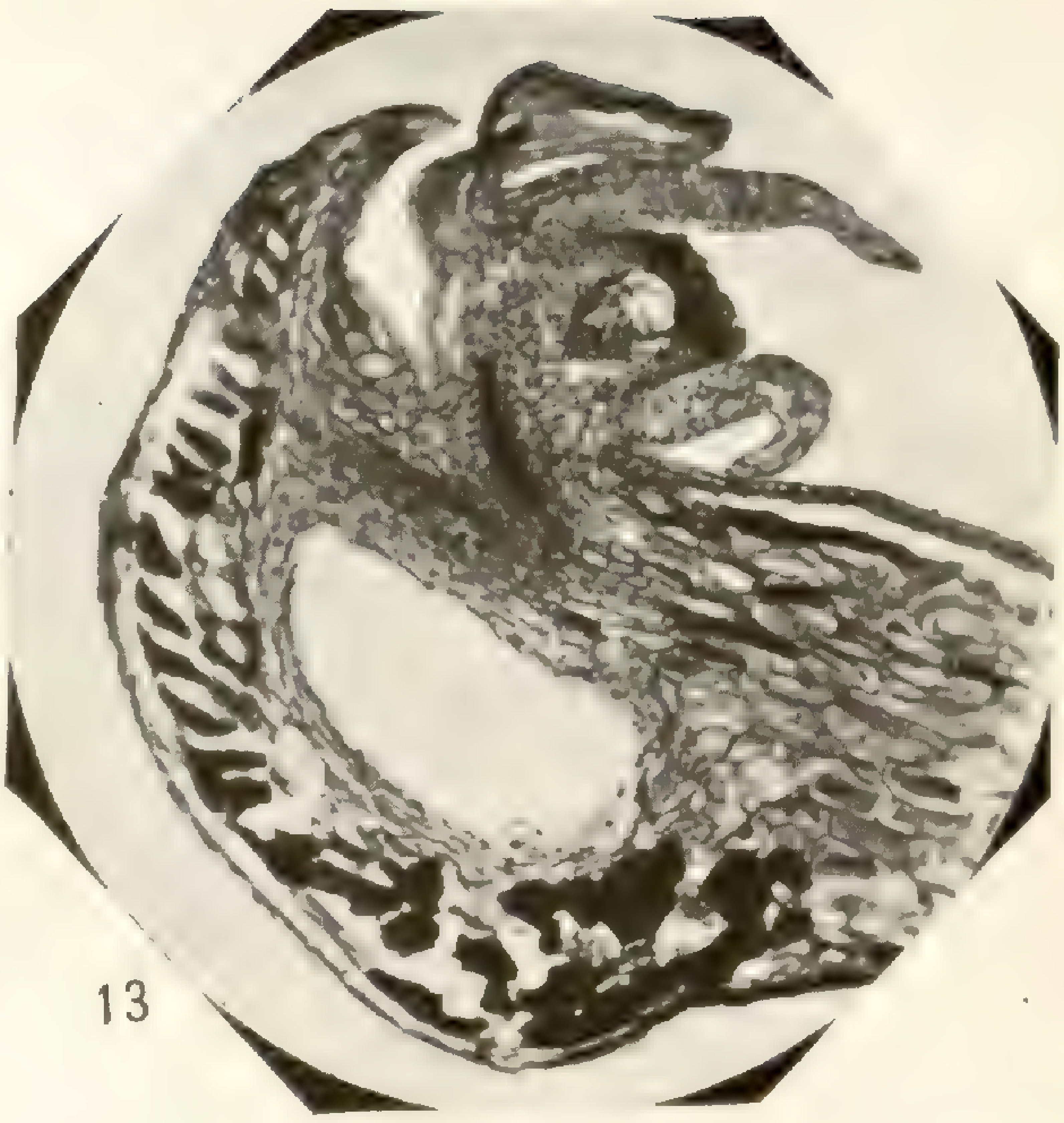
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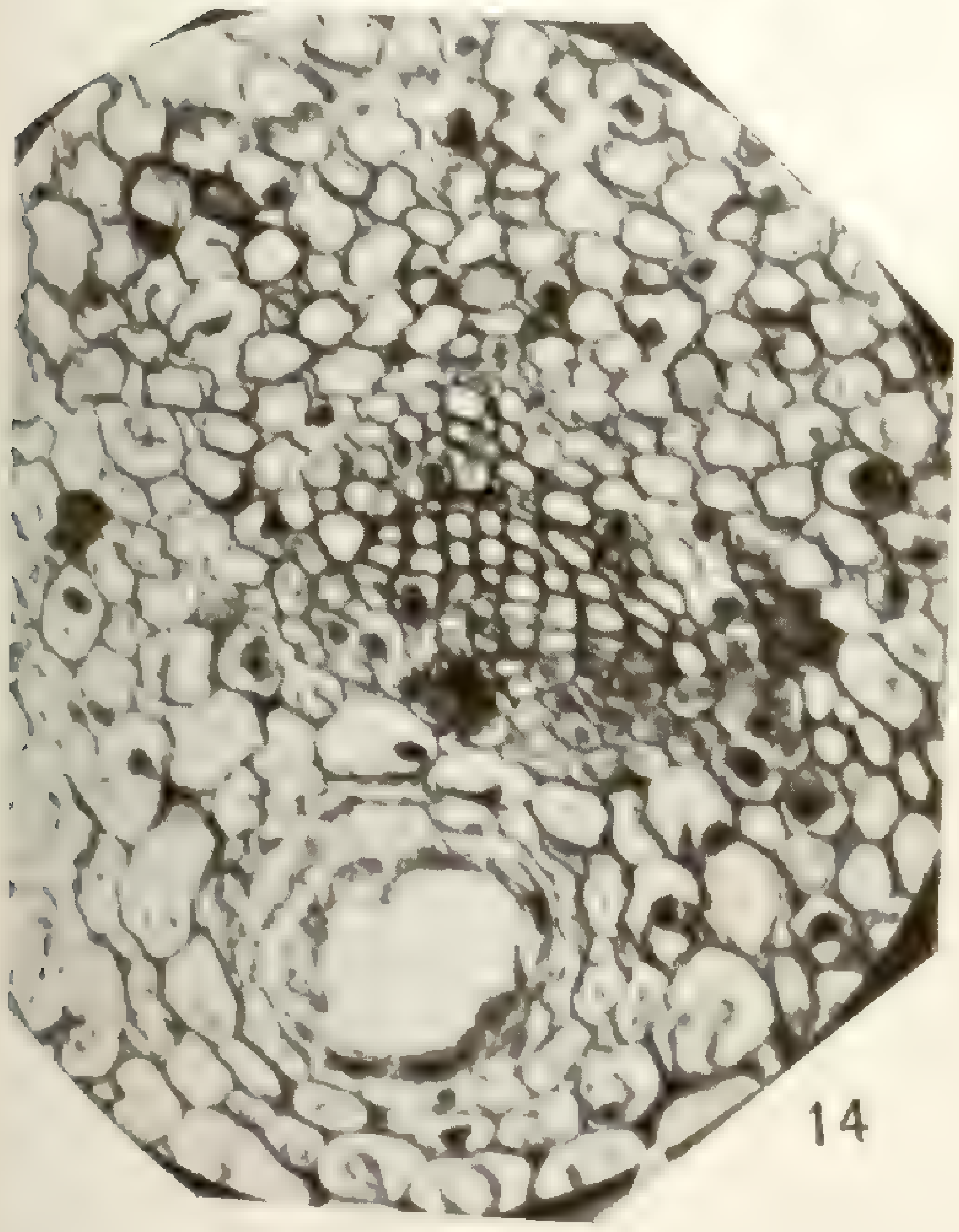
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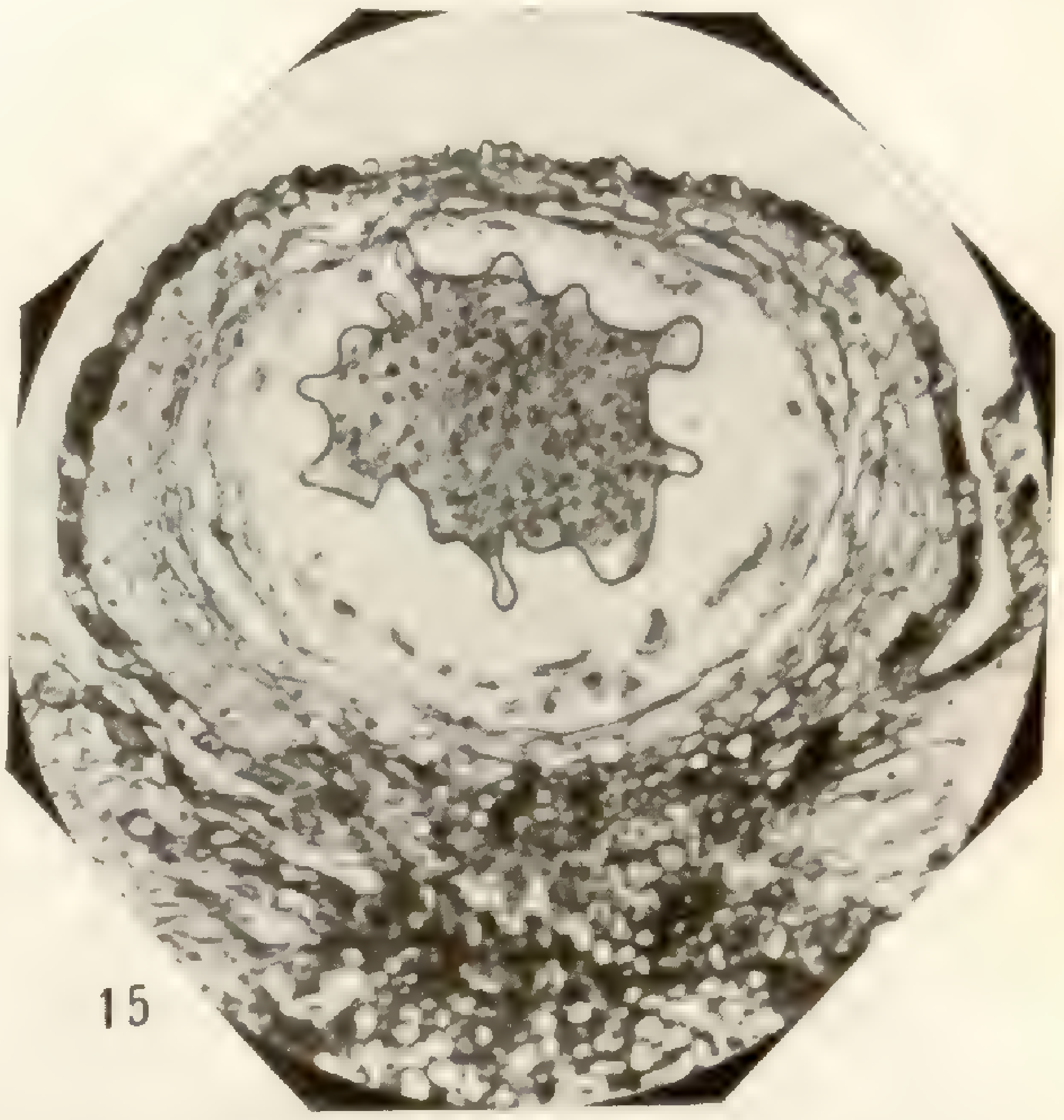
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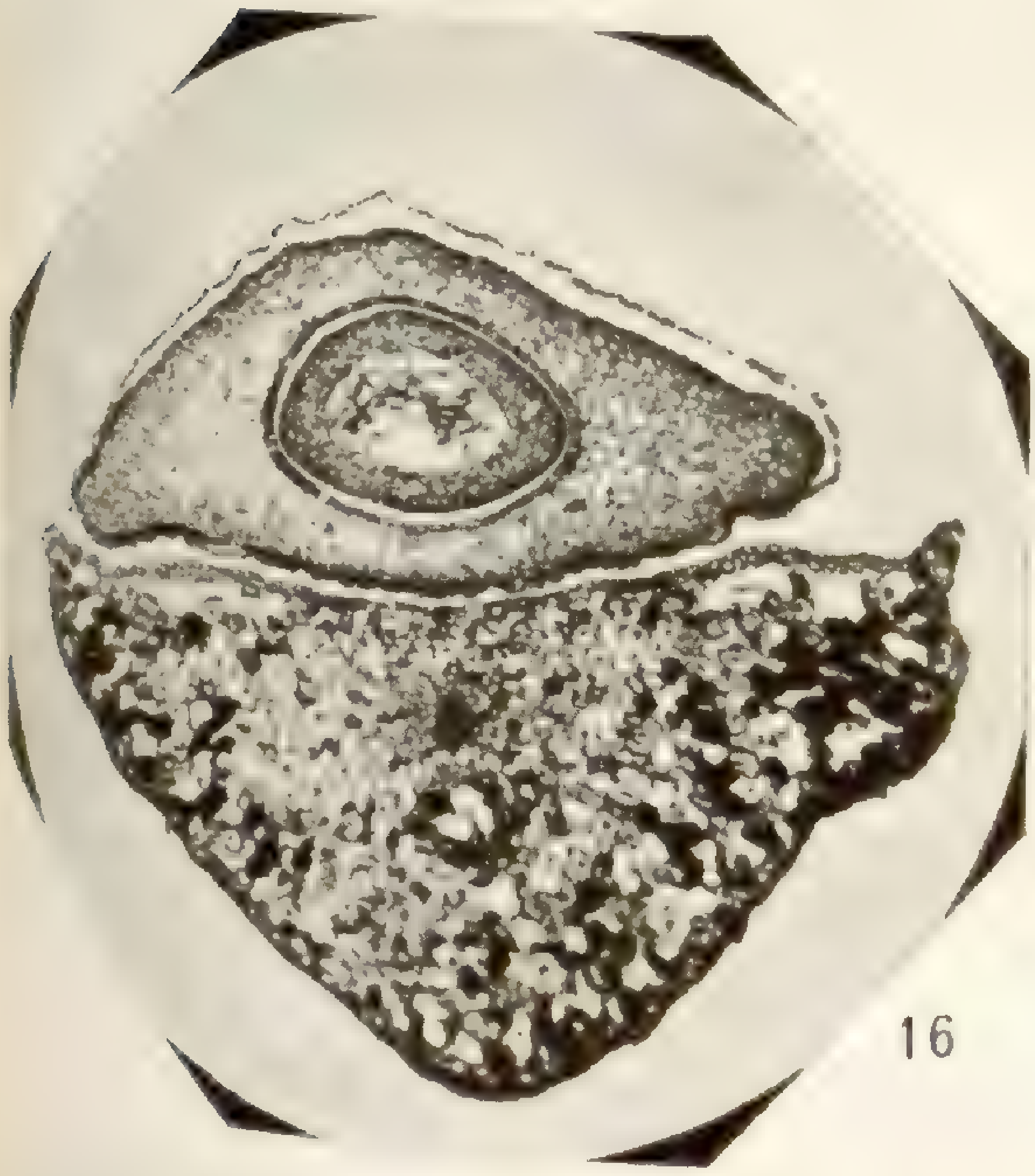
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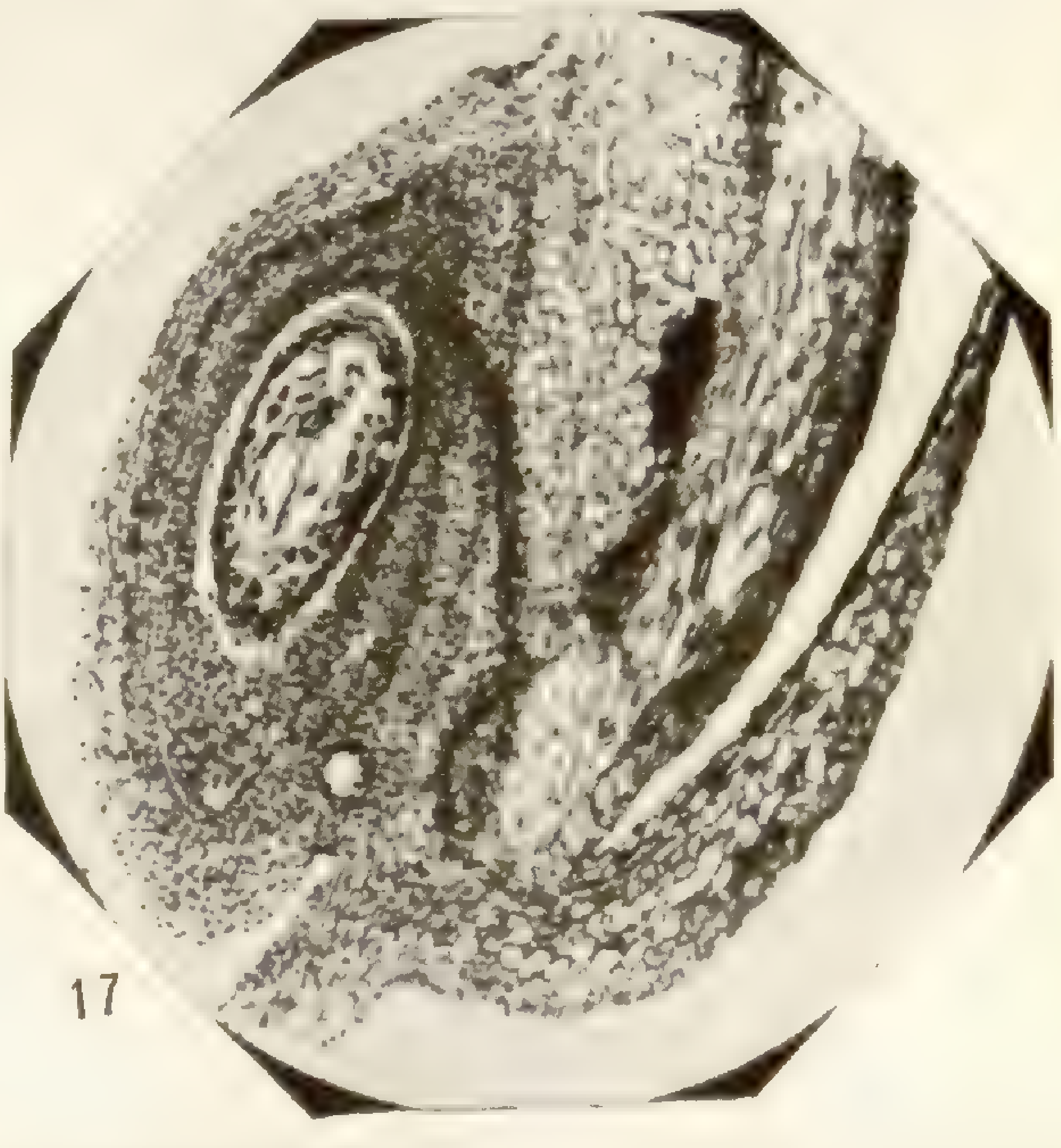
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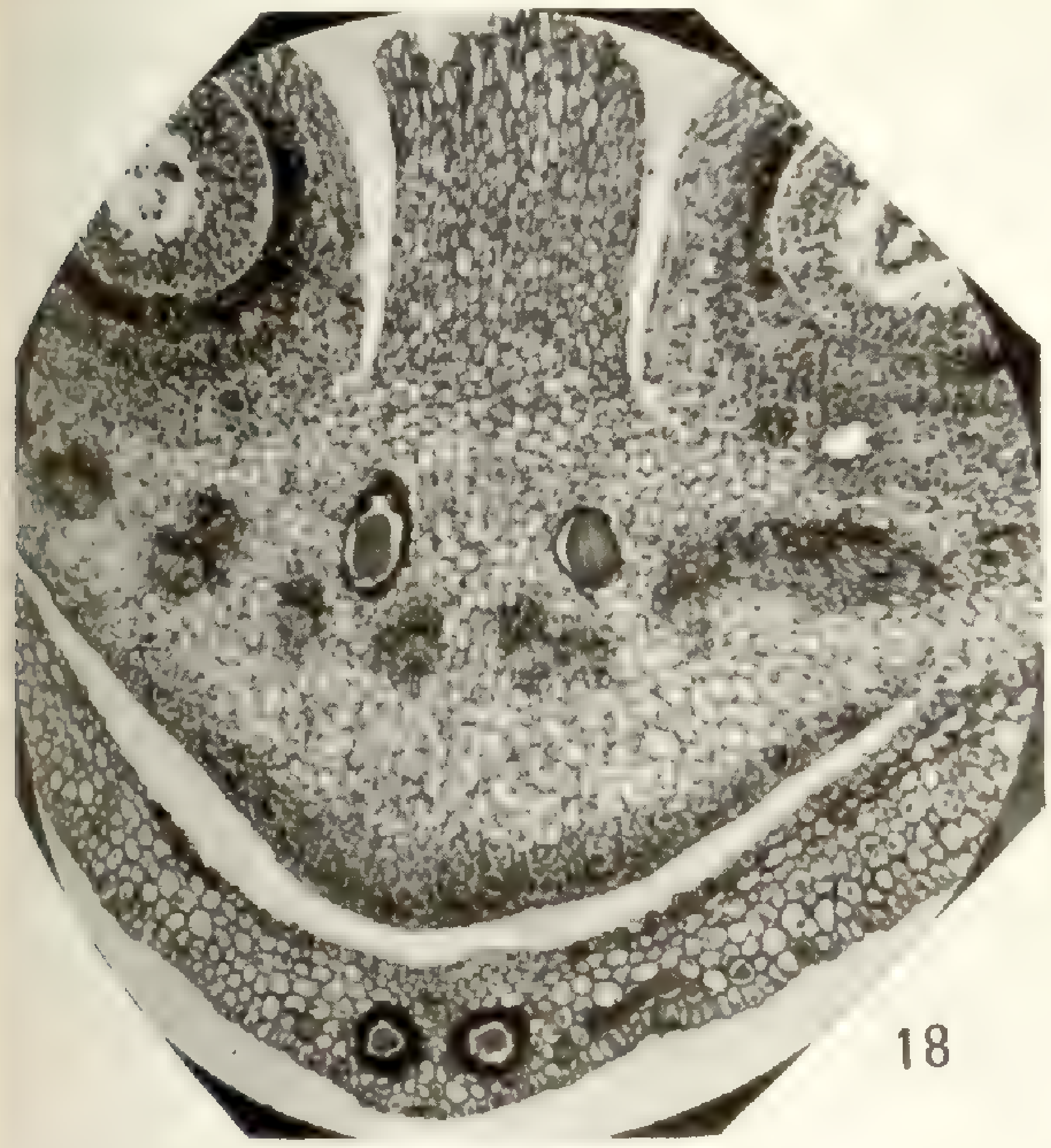
THOMSON on MEGASPOROPHYLL



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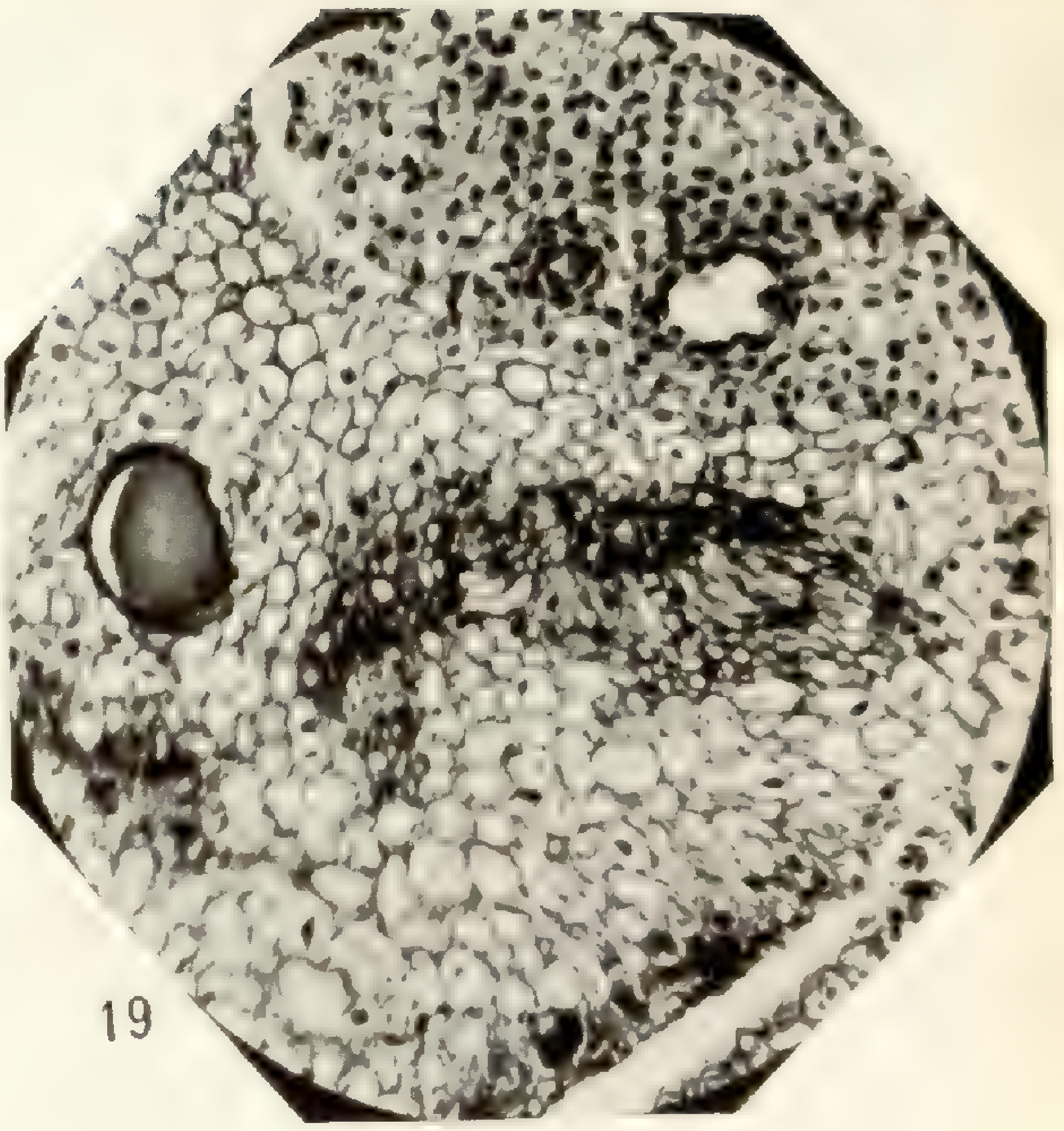

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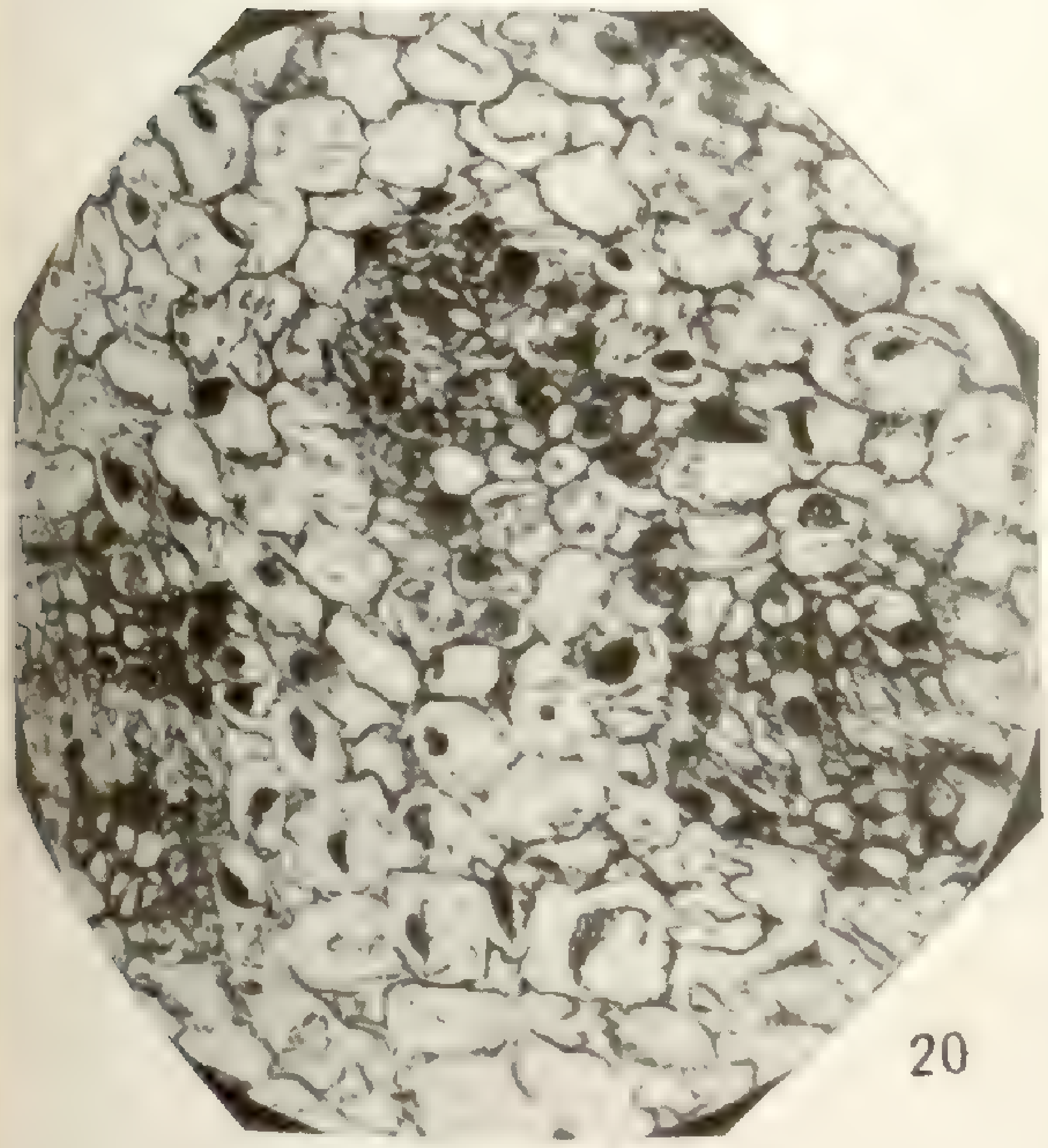

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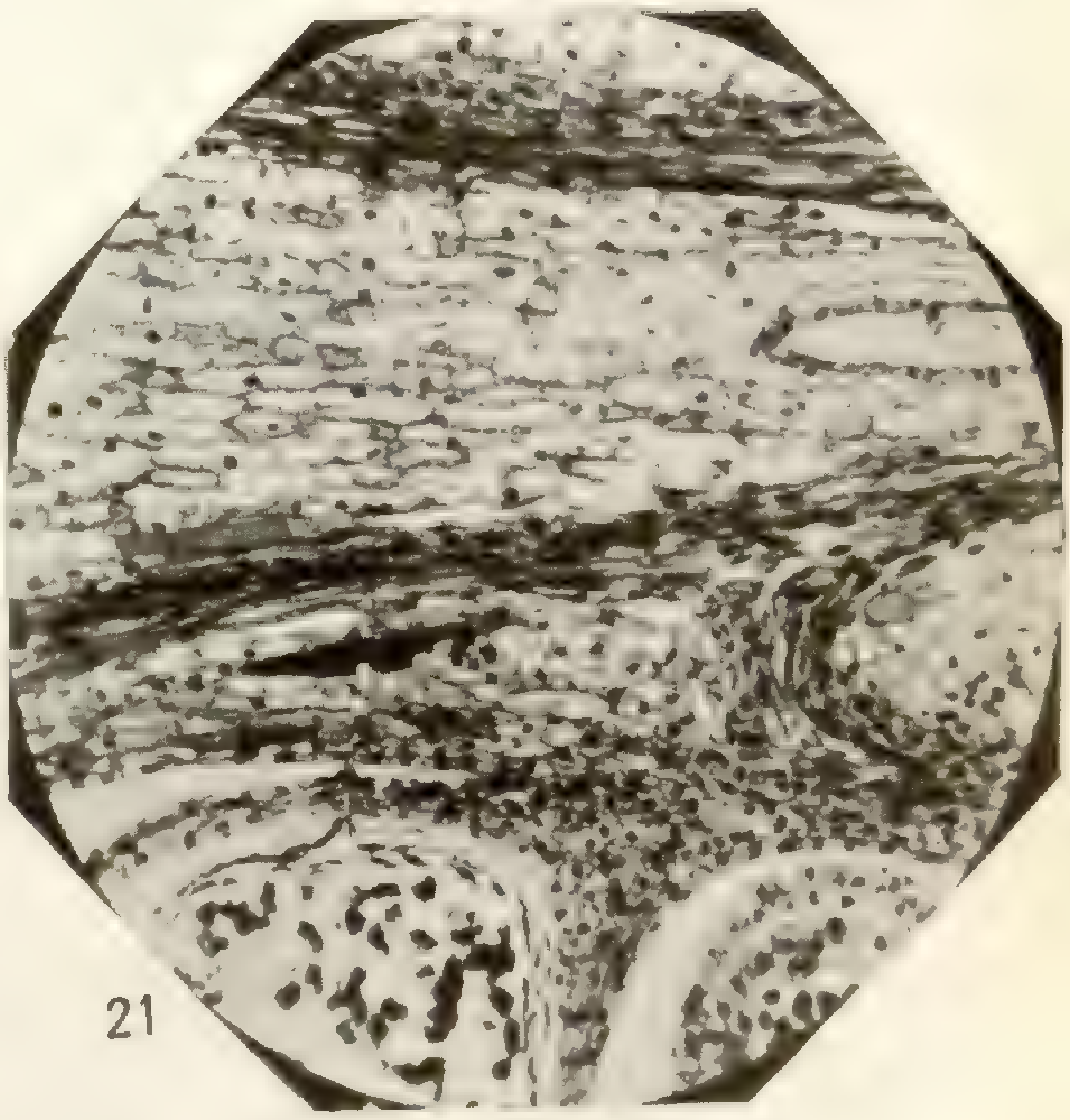

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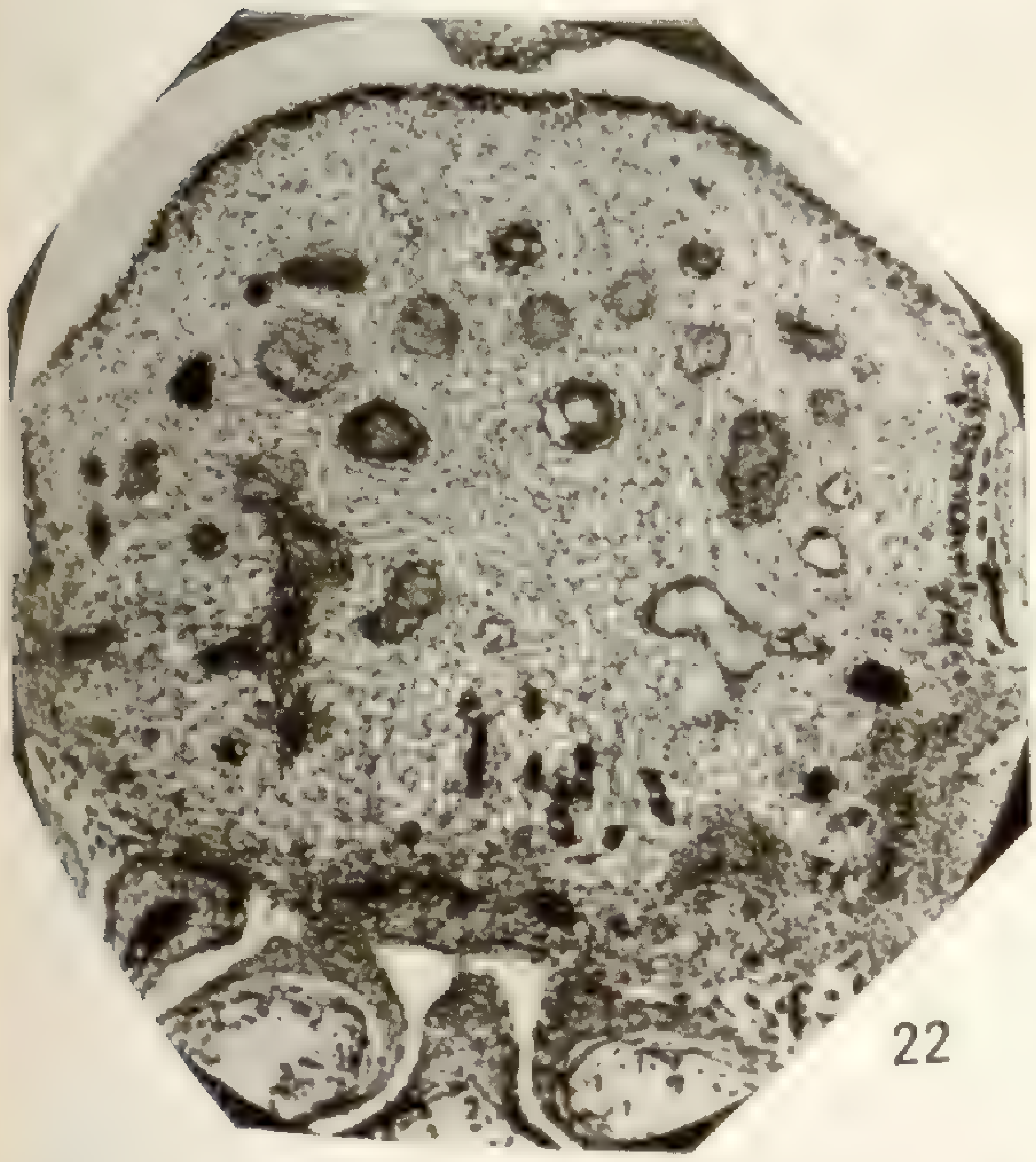

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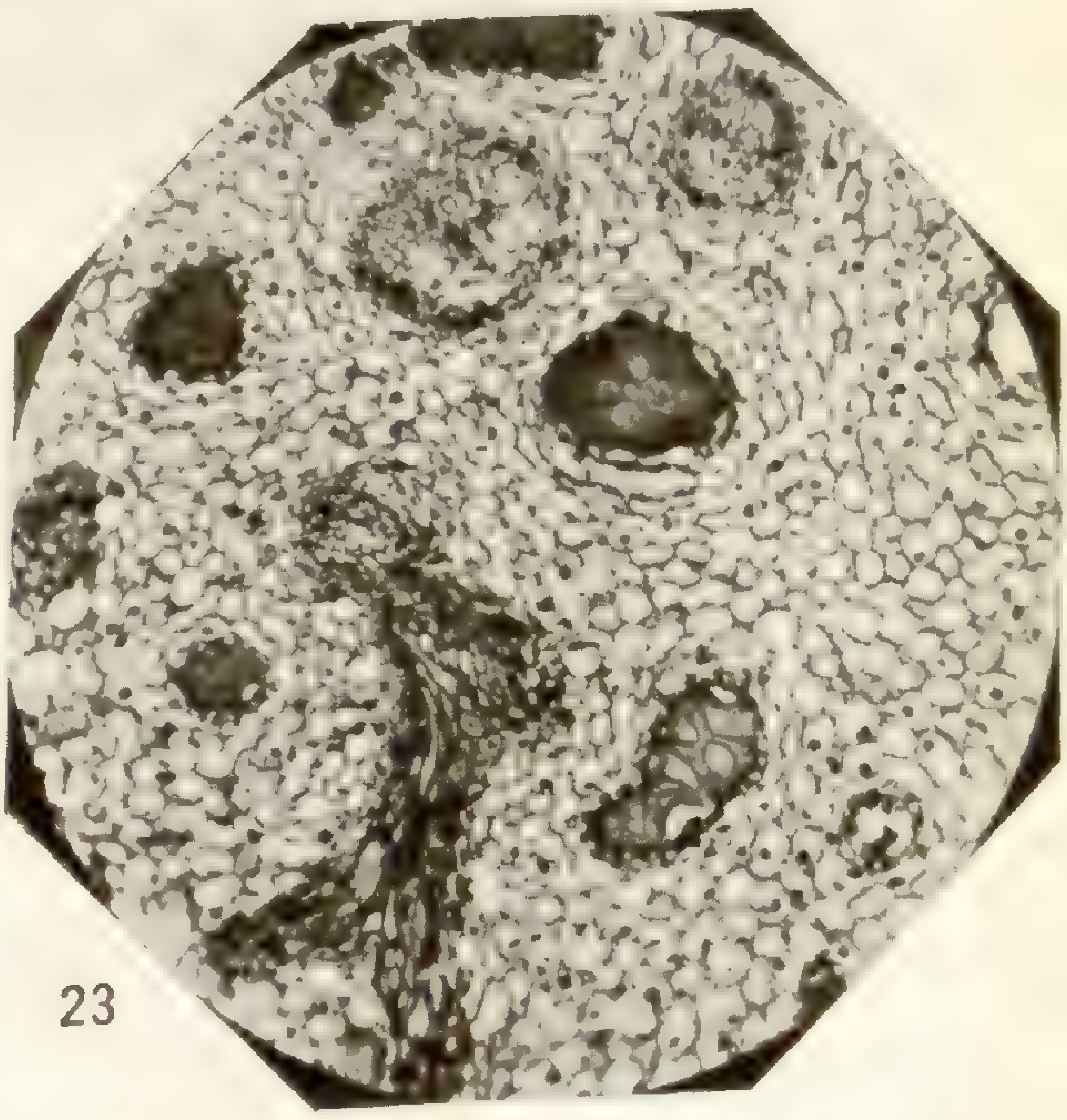

23

THOMSON on MEGASPOROPHYLL

STUDIES ON THE OXIDIZING POWER OF ROOTS[1]

OSWALD SCHREINER AND HOWARD S. REED

The present paper embodies a series of studies upon the oxidizing powers of plant roots grown in aqueous extracts of soils and in solutions of various compounds. The results, it is believed, throw some light on the action of plants upon the soil and indicate how soil conditions affect certain functions of the plant.

The experiments which are presented show that plant roots are able to carry on active extra-cellular oxidation, chiefly by means of the enzymes which they secrete. From the standpoint of root excretions the study is of interest because it has often been supposed that the roots of growing plants excrete organic and inorganic acids which aid in the solution of soil minerals. The idea undoubtedly owes its prevalence largely to the experiments of LIEBIG[2] and of SACHS[3] which demonstrated the corrosion of polished marble plates by growing plants. The more recent investigations upon the subject made by CZAPEK,[4] KOSSOWITCH,[5] and KUNZE[6] have shown, however, that very little acid is excreted by the roots of the higher plants, and that the results of the earlier workers were mainly due to the action of carbon dioxid.

This oxidizing power of plants gives them an important action upon the soil. Whether they have the power to oxidize the inorganic constituents of the soil remains to be determined; but it has been shown that they are able to oxidize organic substances, such as the chromogens employed in these experiments, at a fairly rapid rate. If these substances are oxidized, it is only logical to conclude that the organic substances occurring in the soils are also oxidized by the action of plant roots.

This oxidation of organic compounds is of additional interest in the light of recent investigations, which show that the cause of unproductivity in certain soils is due to the presence of toxic organic compounds.[7] The beneficial effect of oxidation in such soils may be inferred from the results of thorough tillage, involving sub-drainage and cultivation, since these operations promote aeration of the soil with subsequent increase in growth of roots and microorganisms. Under such conditions experience has shown that the organic substances in the soil are most completely converted into substances commonly known as humus. It is certain that the oxidizing activities of the soil and plant play a significant part in this important process.

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[1] Published by permission of the Secretary of Agriculture.

[2] Annalen Chem. Pharm. **105**:139. 1858.

[3] Bot. Zeit. **18**:117. 1860.

[4] Jahrb. Wiss. Bot. **29**:321. 1896.

[5] Ann. Sci. Agron. II. **8**:220. 1903.

[6] Jahrb. Wiss. Bot. **42**:357. 1906.

PREVIOUS WORK

The existence of an oxidation process in soils has long been known. Without apparently understanding the precise cause of this phenomenon, LIEBIG pointed out its importance for productive soils, and, according to the same author, the phenomenon had been earlier investigated by INGENHOUSS and DE SAUSSURE. Among the more modern investigations on the processes of oxidation in soils the works of DEHERAIN and DEMOUSSY,[8] WOLLNY,[9] RUSSELL,[10] and DARBISHIRE and RUSSELL[11] should be mentioned. These investigations are all along the line of bacterial activities in the soils. Recent studies by KÖNIG,[12] however, furnish evidence of a catalytic power of soils due to the presence of an enzyme.

The literature dealing with the oxidizing power of plant juices is already voluminous. Within recent years, our knowledge of processes going on within the plant has been greatly extended by the studies which have been made upon oxidizing enzymes. Since several comprehensive and instructive summaries of work on this subject have appeared, among which may be mentioned those of BACH and of CZAPEK'S *Biochemie*, it is unnecessary in the present paper to review what has been done in this rapidly developing field.

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[7] Jour. Amer. Chem. Soc. **30**:1295, 1599. 1908. Bur. Soils, U. S. Dept. Agric. Bulls. 36, 40, 53.

[8] Annales Agron. **22**:305. 1896.

[9] Die Zersetzung der organischen Stoffe und die Humusbildung. Heidelberg. 1897.

[10] Jour. Agr. Sci. **1**:261. 1905.

[11] Jour. Agr. Sci. **2**:305. 1907.

[12] Landw. Versuchsst. **63**:471. 1906; **66**:401. 1907.

The study of the oxidizing enzymes which are given off by the roots of plants, i. e., extra-cellular oxidation, has received less attention, and it is to this particular field that the present study belongs.

Molisch[13] appears to have been the first to demonstrate the oxidizing power of root secretions and to show their enzymotic nature. He found that the root secretion was capable of oxidizing various organic substances, such as guaiacol, pyrogallol, and gallic acid. His work showed that there was considerable active secretion on the surface of growing roots, and that this secretion had definite powers to effect changes in organic substances.

Czapek,[14] in making a general study of root secretions, followed some of the investigations made previously by Molisch. From experiments upon the action of seedling roots upon starch paste and sugar solutions, he regarded it probable that the growing roots produce only diastase or inverting ferments, although exact proof could not be offered. He believed, however, that the experiments of Molisch failed to prove the production of oxidizing enzymes by roots.

The ideas of the oxidizing powers of roots set forth by Molisch are well corroborated by the investigations of Raciborski[15] upon the oxidizing powers of plant tissues.

In his work reagents were used which were so nearly non-toxic that they could be added to solutions in which plants were grown. In some experiments the reagents were added to water cultures containing the growing plants; in others, strips of filter paper which had been saturated with the reagent were applied to the surface of growing roots. The substances used for showing the oxidizing power of growing roots were α-naphthylamine, benzidine, phenolphthalin, ferrous ammonium sulfate, Barbadoes aloes, guaiac, phloridzin, pyrogallol, leucomethylene blue, etc.

The extra-cellular oxidation by the roots of the phanerogams studied was found to be strongly localized and limited to the absorbing surface of the root. The most intensive oxidation occurs in the region covered by the root hairs. After the death of the root hairs, as the root grows older, the oxidation becomes weaker (as shown by the less intense coloration) and vanishes in basipetal order. The short growing zone of the root between the root cap and the region of root hairs shows very little if any oxidation. The cells of the root cap behaved differently in different plants. In some there was a very weak oxidizing power, insignificant in comparison with that of the absorbing region of the root; in other plants the root cap showed no power to oxidize. This observation is the more interesting because PFEFFER[16] regarded the experiments of MOLISCH to lack proof that the guaiac-bluing power was due to living cells and not to the dead or dying cells of the root cap.

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[13] Sitzb. Akad. Wiss. Wien. Math. Nat. Kl. **96**:84. 1888.

[14] Jahrb. Wiss. Bot. **29**:321. 1896.

[15] Bull. Acad. Sci. Cracovie **1905**:338, 668, 693.

The oxidation which occurred in naphthylamine and benzidine solutions first appeared on the outer surfaces of the walls of the root hairs and epidermal cells, later in the wall itself, and finally in the outer layer of the ectoplasm. When roots were left for a long time in a solution of these chromogens, the entire protoplasm of the epidermal cells and root hairs gradually assumed the dark color of the oxidized chromogen, although it was not determined whether this color was due to the diffusion inward of the dye formed at the surface, or to an actual intracellular oxidation.

MATERIAL AND METHODS

The experiments described in succeeding pages consisted in studying the oxidizing power of wheat plants grown under various conditions in connection with soil-fertility investigations. It was necessary to grow the wheat plants used for experimentation in solutions, since in such cultures it is possible to observe the oxidation without disturbing the roots. For the study of soil conditions an aqueous extract was made by stirring one part of soil with five parts of distilled water for three minutes and filtering after 30 minutes through a Pasteur-Chamberland clay tube. It has been found that soil extracts prepared in this manner possess a plant-producing power similar to that of the soil from which they were made. In other words, fertile soils yield extracts which promote good plant growth, and infertile soils give extracts producing poor plant growth.

The water used in making solutions and soil extract was the ordinary laboratory distilled water treated with carbon black. The water was distilled from a copper boiler, condensed in a block-tin worm, and collected in a tin-lined copper tank. This method of distillation gives very good water for ordinary chemical work, but does not free it from traces of volatile organic compounds, which may exert a toxic action as was described by LIVINGSTON[17] and the writers.[18] It has been found that these deleterious substances may be effectually removed by treating the distilled water with some finely divided solid which possesses a strong absorbing power, such as ferric hydrate, or carbon black. The procedure usually followed was to shake up a small quantity of the carbon black in the water and let it stand for 30 to 60 minutes; at the expiration of that time the water was filtered through ordinary filter paper and was ready for use. This treatment has been found to be as efficient in producing physiologically pure water as redistillation with strong oxidizing agents, like acid potassium bichromate or alkaline potassium permanganate.

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[16] Abhandl. kön. säch. Gesells. Wiss. Leipzig, Math. Phys. Cl. **15**:375. 1889.

The varieties of wheat used in the experiments were "Chul" and "Harvest Queen." The seeds were germinated on floating perforated plates, according to the method described by LIVINGSTON[19] and in Bulletin 40 of this Bureau. The seedlings were transferred from the perforated germinating plates to the cultures just as the first true leaf was beginning to emerge from its sheath.

The plants were held in notches cut in the edge of a cork, as described by LIVINGSTON. In this way the seed in which enzymes were acting upon reserve food materials were kept out of the solutions and the enzyme effects observed were ascribable to substances arising from the roots.

Salt-mouth bottles, having a capacity of 250^{cc}, were used as culture jars, and ten wheat plants were grown in each jar. In each test two cultures containing 20 wheat plants were usually employed, and comparison was made with an equal number of plants growing in pure distilled water under the same conditions. All experiments were conducted in a greenhouse. During the season of the year in which conditions were most favorable for growth, each experiment was conducted for 8 to 12 days before studying the oxidizing action of the plants, but during the cloudy winter weather the time was sometimes extended to 14 to 16 days.

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[17] Bur. Soils, U. S. Dept. Agr. Bull. 36. 1907.

[18] Bur. Soils, U. S. Dept. Agr. Bull. 40. 1907.

[19] Plant World **9**:13. 1906.

In addition to determining the oxidizing power of the plants subjected to various treatments, their growth was estimated by recording the green weight and transpiration of each culture.[20]

SUBSTANCES CAPABLE OF SHOWING THE OXIDIZING POWER

Two classes of substances have been found useful in showing the oxidizing powers of plant roots in solution cultures. The first class comprises certain soluble chromogens, which yield, upon oxidation by the plant roots, insoluble colored compounds mainly deposited upon the surface of the roots. The oxidation is usually rapid enough to produce marked results before the surface extension of the roots perceptibly disturbs the zonal distribution of the colors. The second class of chromogens consists of certain substances which give soluble coloring matters as the result of the oxidizing action of the roots. The oxidizing action may be shown by the change from a colorless to a colored compound, or by a change from one color to another and distinctly different color.

Compounds belonging to the first class which have been used in this work are *a*-naphthylamine, benzidine, vanillin, vanillic acid, and esculin.

Alpha-naphthylamine is only slightly soluble in water, but constitutes a good reagent for use in plant cultures because its colorless solution is non-toxic, or nearly so, to plants. When oxidized by the roots of plants, or by reagents such as ferric chlorid or silver nitrate, *a*-naphthylamine is converted into the insoluble, lavender-purple oxynaphthylamine. When the oxidation is performed by the growing roots of a plant, the oxynaphthylamine is deposited upon the surface of the roots in characteristic zones, as already described by RACIBORSKI (*op. cit.* 357). The root cap is slightly if at all colored; the zone of primary meristematic cells immediately back of the root cap is marked by a distinct narrow band of color; the zone of actively growing cells in the region of greatest elongation is not intensively colored; the more slowly growing portions of the root possess the purplish color, but it becomes less intense as one passes to the upper parts of the root.

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[20] For a discussion of the value of these criteria the reader is referred to LIVINGSTON, BOT. GAZETTE **40**:178. 1905; JENSEN, BOT. GAZETTE **43**:11. 1907; and Bureau of Soils, U. S. Dept. Agric. Bull. 47. 1907.

The superior oxidizing power of the meristematic tissues of the plant is not only shown by the narrow zone of deep color formed on the primary meristem of the apical portion of the roots, but also by the small dots of color produced on that portion of the root from which secondary roots arise. If a wheat root 8 to 10^{cm} in length is placed in a solution of naphthylamine it will exhibit, in addition to the deeper colored zones near the apex, dark-purple spots at the places where secondary roots are forming and are about to break through the cortical layers of the primary root. If secondary roots are already present they show the same zones of colors already described for the primary roots.

The concentrations of naphthylamine used in solution cultures are necessarily low on account of its slight solubility in water, but are sufficiently strong to show the oxidation. In ordinary practice 10 parts of naphthylamine to a million (10^{mg} per liter of water) is a suitable concentration to use. This concentration will eventually retard the growth of wheat plants, but is not detrimental to growth in the length of time usually required to demonstrate the oxidizing powers of the plant roots. A concentration of 5 parts per million sometimes acts as a stimulant to growth.

Benzidine is another chromogen, which is oxidized by plants and may advantageously be used to demonstrate their oxidizing action. It is only slightly soluble in water, but in weak, colorless solution it is readily oxidized by plant roots to an insoluble dye which gives the roots a blue-black or black appearance. Benzidine is slightly toxic to plant growth, but does not cause pathological conditions within the time required for demonstrating the oxidizing power of the plant roots. A concentration of 5 parts benzidine to a million of water will give good results and does not injure wheat roots in 24 hours, although that concentration may eventually inhibit growth.

The effect of oxidation may easily be demonstrated by allowing the roots of wheat plants to grow in a 5 parts per million solution of benzidine for 12 to 24 hours. The formation of colors in distinct zones is fully as striking as in the case of *a*-naphthylamine. As before, the root cap does not produce oxidation products, the primary meristem is marked by a narrow band of brown color, the zone of elongation is practically uncolored, whereas the portion of the root just above the zone of greatest elongation is entirely colored blue-black or black by the oxidation products.

Solutions of vanillin and vanillic acid act in much the same manner as those of naphthylamine or benzidine, but the concentrations required to demonstrate the oxidizing power of roots are quite strongly toxic.[21] Both substances are converted by the oxidizing action of the roots into a purple insoluble dye which stains the surface of the roots in the manner previously described. The concentration of vanillin in the solution most favorable for showing oxidation with wheat plants lies between 250 and 500 parts per million. A solution of this concentration will demonstrate the oxidizing power of the roots before the plants become seriously injured. To demonstrate the oxidizing power of roots with vanillic acid, a solution of the latter containing 25 to 50 parts per million should be used.

Esculin is another chromogen belonging to this class, but was found to be less suitable for this work. Esculin solutions, when freshly prepared, exhibit a blue fluorescence. After plant roots have grown for a few days in such a solution, the blue fluorescence is lost, and the roots themselves are colored yellow as a result of their oxidizing activity, the dye formed being insoluble and remaining upon the surface of the roots where the greatest oxidation occurs. The concentrations necessary to demonstrate the oxidizing power of roots range from 500 to 1000 parts per million, and are eventually quite toxic to wheat plants.

The second class of chromogens, viz., those which are converted into soluble coloring matters, are in many respects more useful for oxidation studies than those belonging to the first class, because the intensity of the color, and hence the amount of oxidation, can be quantitatively expressed. The substances belonging to the second class which have been employed in this study are phenolphthalin, aloin, and leuco-rosolic acid. Alcoholic solutions of guaiac were also used for various tests, but could not be put into solution cultures containing growing roots.

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[21] Bur. Soils, U. S. Dept. Agric. Bull. No. 47. 1907. Proc. Soc. Biol. Chem 1:33. 1907. Bot. Gazette 45:73. 1908.

The value of phenolphthalin, a leuco-compound prepared from phenolphthalein, as an indicator of oxidizing enzymes, has been demonstrated for plant work by KASTLE[22] and by RACIBORSKI.[23] Phenolphthalin is prepared by the method described by BAEYER,[24] which consists in reducing ordinary phenolphthalein with zinc dust and sodium hydroxid to phenolphthalin. The latter substance is oxidized back to phenolphthalein by the oxidizing power of the plant roots, a change which is readily demonstrated when the solution is rendered alkaline. The following procedure was observed in preparing this reagent. Weigh out 250^{mg} of phenolphthalein, 3^{gm} of sodium hydroxid, and 4 or 5^{gm} of zinc dust. Place all in a flask and add 100 to 150^{cc} of water. Place the flask on a sand bath and heat sufficiently to cause a rapid evolution of hydrogen, without causing the contents of the flask to boil violently. The heating usually requires 2 to 3 hours to effect reduction of the phenolphthalein. The contents of the flask, after reduction is completed, may be filtered and rendered nearly neutral with hydrochloric acid, and may then be used as an indicator in the plant cultures. However, better results may be obtained by using phenolphthalin purified according to the method given by BAEYER. After purification the phenolphthalin is dissolved in $N/10$ or $N/20$ NaOH and a few cubic centimeters of the alkaline solution put into each culture, adding equal amounts to cultures which are to be compared. If quantitative results are desired, it is necessary to reduce all the solution cultures to neutrality or the same degree of alkalinity. A very slight degree of alkalinity is not usually harmful to plants within the duration of an experiment, and is favorable to the process of oxidation. Phenolphthalin is slowly oxidized by mere contact with the air; therefore it is advisable to instal controls which will allow the results to be corrected for this atmospheric oxidation. When the phenolphthalin is added to the solution cultures, a like quantity is therefore added to jars of distilled water equal in volume to the cultures. The amount of oxidation in these blanks is subtracted from what is observed in the plant cultures.

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[22] Amer. Chem. Jour. **26**:526. 1901. Hyg. Lab. U. S. Pub. Health and Mar. Hosp. Ser. Bull. 26. 1906.

[23] Bull. Acad. Sci. Cracovie, Math. Nat. Cl. **1905**:338.

[24] Annalen Chem. **202**:80. 1880.

Plant cultures usually show striking results at the end of 10 to 20 hours, depending somewhat upon the temperature and amount of root surface. At the end of the experiment the plants are removed from the cultures, and all are rendered distinctly alkaline with sodium hydroxid solution, and thus the red phenolphthalein color appears.

The great advantage in the use of phenolphthalin to demonstrate the oxidizing power of roots lies in the fact that it is capable of yielding quantitative results. After the colors have been developed in the alkaline solution, their intensities may be estimated by the aid of a colorimeter. In the work reported below the color intensities were estimated by means of the colorimeter previously described,[25] which permits of rapid and accurate readings. The colored solutions may be read against a standard phenolphthalein solution or against a standard Lovibond red glass slide.[26] The readings of the colorimetric tubes are inversely proportional to the color intensity and are easily reduced to their relative values.

Aloin is a substance which may be used to demonstrate the oxidizing power of roots in the same way as phenolphthalin is used. Aloin, or barbaloin, is the active principle of Barbadoes aloes, and is obtained in the market in the form of a yellow powder, fairly soluble in water and serving well as an indicator of the oxidizing power of plants. At the concentrations used in our work it was not found to exert any toxic action upon plants. As a result of a limited investigation of the chemistry of aloin, it seems that its value as an indicator of the oxidizing power of plants depends largely upon the content of iso-barbaloin.

When oxidized by the plant roots, the aloin solution is changed from a pale yellow color to a permanent deep wine-red color, similar to that given by KLUNGE's reaction for iso-barbaloin. KLUNGE's reaction[27] consists in dissolving aloin (containing iso-barbaloin) in a 15 per cent. sodium chlorid solution and adding 5^{cc} of concentrated copper sulfate solution. Almost immediately the straw-yellow solution begins to change to a permanent deep wine-red. The change is hastened by warming the solution.

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[25] Jour. Amer. Chem. Soc. **27**:1192. 1905. Bur. Soils, U. S. Dept. Agric. Bull. 31, 1906.

[26] LOVIBOND, Jour. Soc. Chem. Ind. **13**:308. 1894; see also SCHREINER, Pharm. Rev. **19**:61. 1901.

[27] Schweizerische Wochenschr. Pharm. **21**:1. 1883; also Leger, Compt. Rend. Acad. Sci. Paris **131**:55. 1900.

When experimenting with plant juices containing enzymes, there appears to be a difference between the reactions to aqueous and alcoholic solutions of aloin. As the result of experiments described in detail in a subsequent section of this paper, it was found that an aqueous solution of aloin is a better indicator of the presence of oxidase, while an alcoholic solution of aloin is the better indicator of peroxidase.

Aloin, like phenolphthalin, should be added to neutral or faintly alkaline culture solutions, and where quantitative results are desired all solutions should be of the same degree of alkalinity. In all of our work aloin was added at the rate of 100^{mg} of aloin to 250^{cc} of culture solution. If actively growing seedlings are used in a very faintly alkaline solution, a small amount of red color may be developed in an hour or two, but the experiments should be continued for 12 to 20 hours for the final observation. When certain inorganic salts were present in the culture solutions, the aloin red color was slightly modified. The addition of nitrates or previous treatment of the soil extracts with an absorbing agent gave the oxidized aloin a purplish tinge, resembling that of fresh fuchsin solution. The presence of calcium carbonate gave a purer red color, resembling alkanna or cochineal solution.

The fact that aloin is changed by oxidation from a light yellow to a deep red solution makes it somewhat more difficult to obtain colorimetric readings than in the case of phenolphthalin, where there is a change from a colorless to a red solution. Nevertheless, it is practical to use the colorimeter for measuring approximately the intensity of color in aloin solutions, by arranging the solutions in the order of their apparent color intensities, and using each solution first as an unknown and then as a standard for the next higher. For example, let No. 1, the weakest color, be the standard against which No. 2 is read. Then discard No. 1; set No. 2 at a convenient mark, and, using it as the standard, read No. 3. In turn No. 3 is used as the standard for No. 4, and so on. In this way one avoids the necessity of comparing a solution strongly tinged with yellow against a solution which contains little or no yellow tint. In any two solutions to be estimated the tints of yellow should not be greatly different.

Leuco-rosolic acid is another reagent which is useful for demonstrating the oxidizing power of plant juices[28] and plant roots. When a few cubic centimeters of a slightly alkaline, colorless solution are added to a culture containing plants, the leuco-rosolic acid is oxidized back to rosolic acid, the change being shown by the appearance of the red color. This reagent is not so generally useful as phenolphthalin and aloin, since it is more readily oxidized by mere contact with the air, as well as being more difficult to prepare.

PRELIMINARY EXPERIMENTS

The first experiments were conducted for the purpose of ascertaining some general facts concerning the phenomenon of oxidation by the roots of seedlings, as well as to learn the methods best suited for studying oxidation in soil extracts. The experiments of RACIBORSKI dealt with plants growing under what may be termed pure culture conditions, and those of KASTLE were concerned with the oxidizing power of plant extracts.

In the first experiment, wheat seedlings 4 days old were placed in solutions of α-naphthylamine having concentrations of 1, 2, 5, and 10 parts per million, and in a solution of 5 parts per million benzidine. The experiment was set up at 4 P. M. August 6, and observations were made eighteen hours later. At the expiration of that time colors could be distinctly seen on the white surface of the wheat roots. The roots in the solution of 1 part per million naphthylamine were pale lavender; in 2 parts per million they were pronounced lavender, except at the root cap; in the 5 parts per million solution they were violet in the region occupied by the primary meristem, and in the region of the root hairs where growth of elongation occurs, while the root cap and a narrow zone just above the primary meristem were uncolored; in the 10 parts per million solution the roots showed the same colors as in that of 5 parts per million. The roots in the solution of 5 parts per million of benzidine showed their power of oxidation by the formation of brown-violet color, distributed in the same manner as described for the roots which grew in the solutions of naphthylamine.

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[28] KASTLE, J. H., Hyg. Lab., U. S. Pub. Health and Mar. Hosp. Serv. Bull. 26: 17. 1906.

In order to learn whether the oxidizing powers of roots were affected by conditions which favor growth, and also whether the method used in the first experiment would show such differences, the following experiment was made. Three water cultures were made, in each of which an equal number of wheat seedlings of uniform age and size were employed. One culture was made with redistilled water, the second with an aqueous extract of a rich garden soil, the third with a dilute aqueous extract of well-decomposed stable manure. After the plants had grown for one day in these liquids, the oxidizing powers of the plants were observed by transferring them to other bottles containing 2 parts per million of α-naphthylamine in distilled water. At the expiration of 18 hours the intensity of the purple colors showed that the roots which had previously grown in the extract of garden soil had oxidized more naphthylamine than those which had grown in distilled water, and those which had grown in manure extract had oxidized more naphthylamine than those from the garden soil extract. At the end of 24 hours the differences in color intensity in the two cultures were still more marked.

The next experiment was an attempt to employ a method which would permit a more accurate quantitative expression of the oxidizing power of the roots. Two cultures of wheat seedlings were grown for 5 days in an extract of unproductive soil, under the same conditions as two other cultures in an extract of rich garden soil. Each culture contained 60^{cc} of the respective soil extract. The oxidizing power of the roots in this experiment was shown by using phenolphthalin. The phenolphthalin was prepared by the method given in a previous paragraph, and 0.4^{cc} of the freshly prepared solution were added to each culture of plants after they had grown 5 days in their respective solutions. Nineteen hours after adding the indicator all plants were removed from the cultures and the solutions rendered alkaline, thus producing the phenolphthalein color. The solutions were brought to the same volume by the addition of distilled water, and the relative amount of oxidation was measured by determining the color intensities of the different cultures.

The two cultures of poor soil gave readings of 40 and 42 divisions on the graduated tube against slide No. 2 (Lovibond system); the two cultures of rich garden soil gave readings of 14 and 24 divisions against slide No. 4 (Lovibond system). Averaging the readings and comparing the intensity of the colors, the oxidation in the poor lawn soil and in the rich garden soil stands in the ratio of 1 to 4, or more exactly as 19 to 82. This result indicated that a procedure based upon this method will give satisfactory quantitative results.

This method was further tested by another experiment in which different beneficial treatments were applied to an extract of the unproductive soil used in the last experiment. The results of the last experiment showed that the oxidizing powers of plants growing in solutions of different physiological properties vary considerably, but left the question open as to how much of the oxidation result might be due to plants and how much to the solution. In the present experiment, therefore, two of the four bottles in each set of solutions were left unplanted, and their oxidizing powers measured along with those of the solutions which contained plants. The treatment employed consisted in adding fertilizer substances in the form of pure chemicals. Calcium carbonate was added at the rate of 2000, and sodium nitrate at the rate of 50 parts per million. The cultures were put up August 24 and allowed to grow until August 28, when the amount of water transpired by each culture was ascertained and 3^{cc} of a freshly prepared phenolphthalin solution added to each bottle. The color of the phenolphthalein was brought out by adding a few drops of strong alkali to each culture, and the intensities of the different solutions were compared in the colorimeter. Table I presents the figures which give the relative amount of oxidation in the planted and unplanted solutions. When the phenolphthalin solution was added to the culture jars, the same quantity was added to a jar of distilled water, which served as a control upon the oxidation incident to contact with atmospheric oxygen. The color intensity of the control was determined and subtracted from each of the other readings.

The plants used in this experiment were quite young, and the experiment was only continued for four days, a period rather too short for the maximum oxidation effect, as shown by subsequent experiments; nevertheless, the results show that the different treatments

TABLE I

Relative oxidizing power of cultures and unplanted solutions of Takoma lawn soil extract with and without the addition of fertilizer ingredients. Oxidizing power of plants grown in distilled water used as the basis of comparison (p.p.m. = parts per million).

No.	Solutions	Relative oxidation
1	Distilled water (planted) } Average	100
2	Distilled water (planted) }	
3	Extract Takoma lawn soil (planted)	88
4	“ “ “ “ “	74
5	“ “ “ “ (unplanted)	8
6	“ “ “ “ “	19
7	“ “ “ “ + 2000 p.p.m. $CaCO_3$ (planted)	113
8	“ “ “ “ + 2000 “ “ “	63
9	“ “ “ “ + 2000 “ “ (unplanted)	19
10	“ “ “ “ + 2000 “ “ “	25
11	“ “ “ “ + 50 p.p.m. $NaNO_3$ (planted)	98
12	“ “ “ “ + 50 “ “ “	63
13	“ “ “ “ + 50 “ “ (unplanted)	24
14	“ “ “ “ + 50 “ “ “	17

affected the oxidizing powers. The plants grown in extracts of poor soil possessed less oxidizing power than the controls in distilled water, but the oxidizing power was increased by the addition of calcium carbonate. The addition of sodium nitrate did not show any marked increase to the oxidation in those solutions in the time of the experiment, although its effect as shown in later experiments is always beneficial to oxidation.

The point to be emphasized in this experiment, which has not been previously brought out, is that the soil extract unplanted possesses a comparatively feeble power of oxidation, as shown by the use of phenolphthalin, and that the addition of calcium carbonate and sodium nitrate slightly increased this small oxidizing power.

An additional experiment was performed, using three different salts in distilled water. The results of this experiment, which are given in Table II, confirm those of the foregoing experiment in the soil extract. The cultures were made in duplicate and the figures represent the averages of each pair.

The enzymotic nature of the oxidizing processes was next investigated, using alcoholic guaiac. When alcoholic guaiac is added to a solution in which wheat roots have been growing for a time, evidence of the presence of peroxidase was obtained, but not of oxidase; however, when young growing wheat roots are treated with a solution of alcoholic guaiac they instantly give a blue color, which deepens when hydrogen peroxid is added. This indicates that the cells of the plant root contain an oxidase, as CZAPEK has shown.[29]

TABLE II

Relative oxidizing power of cultures and unplanted solutions of three nutrient salts. Oxidizing power of plants grown in distilled water used as basis of comparison (p.p.m. = parts per million).

No.	Solutions	Relative oxidation
1	Controls in distilled water (planted)	100
2	Solution, 50 p.p.m. of NO_3 as $NaNO_3$ (planted)	282
3	" 50 " " " (unplanted)	39
4	" 35 " K as KCl (planted)	72
5	" 35 " " " (unplanted)	36
6	" 50 " PO_4 as Na_2HPO_4 (planted)	88
7	" 50 " " " (unplanted)	21

A word may be introduced at this place concerning the possible function of bacteria in producing oxidizing ferments which might accomplish some of the effects noted. It is, of course, possible that such organisms existed in the culture employed, since after filtering the extracts no especial precautions were taken to keep them sterile, and microorganisms which were on the roots of the plants would certainly be introduced into the solutions. That these microorganisms were responsible for any appreciable amount of oxidation in the experiments described in this paper is hardly possible. In the first place, the solutions used were not well adapted for a very thrifty development of microorganisms, as was shown by their freedom from turbidity, odors, or other indications. The definite zones of color produced when indicators like *a*-naphthylamine and benzidine were used, and their close correspondence to definite zones of tissue in the root show that the oxidation is performed only by agents intimately connected with the roots. The colors due to oxidation were most intense on the regions of the root where growth was most active, whereas we would expect that the bacteria, if zonally distributed, would be more abundant on the dying cells of the root cap or on the dismantled cortical layers of the older parts of the root. It seems, therefore, highly improbable that the oxidizing activities of microorganisms can be responsible to any appreciable extent for the results observed.

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[29] Annals of Botany **19**:75. 1905.

OXIDATION IN SOIL EXTRACTS

Following the preliminary experiments already described, further experiments were made to study in more detail the oxidizing power of plants grown in extracts of soil of different character. These experiments were chiefly designed to study the oxidizing powers of plants in extracts of good and poor soils, of extracts treated with absorbing agents, and in distillates of soil extracts.

The difference in oxidizing power of plants in extracts of fertile and infertile soils is shown by the following experiments. In the first experiment, an extract of Takoma lawn soil was compared with an extract of good Leonardtown loam. The former is a very unproductive soil, and the latter is a much better and usually a very productive soil. The oxidizing powers of the plants were determined by adding phenolphthalin to the cultures, after the plants had grown in them for nine days. The growth and oxidizing powers of the plants are shown in Table III, relative to control cultures made in distilled water, which are represented as 100 in each case.

TABLE III

Comparative growth and oxidizing powers of plants in extracts of Takoma lawn soil and good Leonardtown loam. Growth expressed in terms of relative transpiration.

No.	Solutions	Relative growth	Relative oxidation
1	Controls in distilled water	100	100
2	Extract Takoma lawn soil	33	72
3	Extract Leonardtown loam	50	286

In the comparatively short time of this experiment during cloudy winter weather, December 10 to 17, the plant growth as manifested by the figures for transpiration did not have time enough to show the relative productiveness of the two extracts, since it has usually been found that the Leonardtown loam extract produces in 14–18 days better plants than distilled water. The figures do show, however, a much greater oxidizing power in the plants grown in the extract of the more fertile soil, even under these conditions.

Subsequent experiments were performed, the results of which corroborated the foregoing. In each case where growth was good, there was also good oxidation; where growth indicated a poor soil extract, the oxidation was small, as will be seen from Tables IV and V.

TABLE IV

Comparative growth and oxidizing powers of plants in extracts of poor sandy loam and garden loam. Growth expressed in terms of relative transpiration.

No.	Solutions	Relative growth	Relative oxidation
1	Controls in distilled water	100	100
2	Extract poor sandy loam	77	103
3	Extract garden loam	125	275

TABLE V

Comparative growth and oxidizing powers of plants in extract of good and poor soils. Growth expressed in terms of relative transpiration.

No.	Solutions	Relative growth	Relative oxidation
1	Controls in distilled water	100	100
2	Extract Arlington clay loam	75	107
3	Extract Clarksville silt loam	123	133
4	Extract Stockton peat	272	400

In all these experiments where direct comparisons are made between the extracts of soils which were so poor as to give less plant growth than pure distilled water, and other extracts giving materially greater growth than the same, it appears to be unmistakably true that the cultures made in extracts of good, fertile soils possess much greater oxidizing powers than those made in extracts of soils of relatively less fertility.

The next question considered was concerned with the effect of treating the soil extract with absorbing agents. Treating the extracts of a more or less unproductive soil with carbon black or other good absorbing agent is usually beneficial to growth. This response seems to be quite general for all poor soil extracts, although their response to other treatments may be quite different. Previous work in this laboratory[30] has shown that this ameliorating action is due to the removal of deleterious organic substances. Extracts were treated with carbon black or ferric hydrate. The absorbing agent was shaken with the soil extract and filtered off at the expiration of a half-hour, in the same manner as the distilled water used in the experiments was prepared. The relative effects of this treatment upon growth and the oxidizing power of the plants is shown in Table VI, where the effect in the untreated soil extract is in each case taken as 100.

TABLE VI

Effect of treatment with carbon black and ferric hydrate upon growth and oxidizing power of plants grown in extracts of various soils. Growth expressed in terms of relative transpiration.

No.	Soil extract	Relative growth	Relative oxidation
1..........	Arlington clay loam*	100	100
	“ “ “ carbon black treated	124	265
2..........	Takoma lawn soil*	100	100
	“ “ “ carbon black treated	137	100
3..........	Alloway clay*	100	100
	“ “ carbon black treated	116	117
4..........	Dunkirk sandy loam*	100	100
	“ “ “ carbon black treated	112	280
5..........	Miami silt loam*	100	100
	“ “ “ ferric hydrate treated	171	198
6..........	Marshall clay loam†	100	100
	“ “ “ carbon black treated	216	130
7..........	Clarksville silt loam†	100	100
	“ “ “ carbon black treated	450	227
8..........	Elkton silt loam†	100	100
	“ “ “ carbon black treated	179	317
9..........	Cecil fine sandy loam†	100	100
	“ “ “ “ carbon black treated	112	200
10..........	Hagerstown loam†	100	100
	“ “ carbon black treated	230	500
11..........	Cecil sandy loam†	100	100
	“ “ “ carbon black treated	193	241
12..........	Dutchess silt loam†	100	100
	“ “ “ carbon black treated	110	373
13..........	Poor sandy loam†	100	100
	“ “ “ ferric hydrate treated	170	534
14..........	Garden loam†	100	100
	“ “ ferric hydrate treated	136	313

* Phenolphthalin used in estimating oxidation.
† Aloin used in estimating oxidation.

It will be noted that in all but one of the soil extracts the effects of the treatment with an absorbing agent strongly increased the oxidizing powers of the plants subsequently grown in the extracts, and the growth of the plants was also increased.

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[30] Bur. Soils, U. S. Dept. Agric. Bulls. 28 36, 40. Jour. Amer. Chem. Soc. **30**: 1295. 1908.

The increased oxidation, as well as the increased growth, points directly to the conclusion that the soil extracts have been so improved by the treatment given as to induce a more active functioning of processes necessary to secure the best conditions for growth. In the single case of No. 2 the growth was increased as a result of the treatment with carbon black, but the oxidation was not. This result was frequently obtained with the Takoma lawn soil; in some cases the oxidizing power was even slightly decreased as a result of treatment with absorbing agents, although growth was increased. No satisfactory explanation has as yet been obtained for this apparently exceptional action. It may be found upon further investigation that the lack of response was due to the presence of matter inhibiting oxidation, which was not removed by the carbon black. This question seems worthy of more study than we have been able to give it.

Extracts of poor soils sometimes contain volatile bodies of a deleterious nature, which can be driven off by boiling and collected in the distillate. The writers have described[31] the behavior of plants grown in such distillates. Where the deleterious bodies are volatile, the distillate usually exhibits the same toxic properties which the original extracts previously possessed, and the residue is correspondingly improved.

To study the effects of these distillates upon the oxidizing powers of the plants the following experiments were made. One liter of such soil extract was placed in a distilling apparatus and distilled until 200^{cc} of distillate had passed over and been condensed. This fluid was made up to 500^{cc} by adding water and designated first portion. When a second 200^{cc} of distillate had been collected, it was likewise made up to 500^{cc} and designated second portion. Cultures were made in each portion, together with controls in pure distilled water. At the end of a week the plants in the different solutions showed marked differences. The plants in the first portion of the distillate were very small and were dying; those in the second portion were much better, in fact, were equal to the controls growing in distilled water. One hundred milligrams of aloin was added to each of the culture bottles, and on the following day the amount of oxidation was noted by comparing the intensity of red color in each culture. The cultures in the first portion showed much less oxidation than either of the other two. The most oxidation appeared to have gone on in the cultures in the second portion, which was slightly in excess of that in the control cultures in pure distilled water.

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[31] Bur. of Soils, U. S. Dept. Agric. Bull. 40. 1907.

The question was studied further, and in a more quantitative manner, by the following experiment. An extract of Elkton silt loam, having a volume of 750^{cc}, was placed in a flask connected with a condenser and distilled. The distillate, amounting to 500^{cc}, was collected in two portions of 250^{cc} each and used as a culture medium in which plants were grown. The residue in the distilling flask, which was diluted to its original volume, was also used for growing plants. For comparison, cultures were also made in the original soil extract. The wheat plants were allowed to grow in the various solutions for 13 days, and then their oxidizing powers were estimated by means of phenolphthalin. The growth and oxidation are shown in Table VII.

TABLE VII

Growth and oxidation in distillate and residue of extract from Elkton silt loam. Growth expressed in terms of relative transpiration.

No.	Solutions	Relative growth	Relative oxidation
1	Original soil extract untreated	100	100
2	First portion of distillate	53	20
3	Second portion of distillate	70	19
4	Residue after distillation, diluted to original volume	132	180

These results show that the distillates of this soil extract were less favorable for growth and oxidation than the original untreated soil extract, while the residue from distillation was materially improved. This seems to indicate that the original soil extract, like others which have been investigated,[32] contained a volatile toxic substance which inhibited oxidation by the roots, and that this substance was driven off by the process of distillation, with resulting benefit to oxidation in the residue. Judging from the growth of the plants, the first portion of the distillate contained a larger proportion of this deleterious substance than the second, although this smaller amount appears to be just as deleterious to the oxidizing powers of the roots as the larger amount present in the first portion. The oxidizing power of the plants in the residue was much greater than in the distillates or in the original soil extract.

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[32] Bur. Soils, U. S. Dept. Agric. Bulls. 28, 36, and 40.

Evidently the oxidizing powers of the roots are affected by certain external conditions, since an improvement in the physiological properties of the soil extract results in increased oxidation, and the presence of deleterious bodies results in decreased oxidation.

From the experimental results thus far presented, it appears that the oxidizing power of the soil extracts themselves can be regarded as partly, but not mainly, responsible for the oxidation observed in the experiments. In one of the preliminary experiments reported in Table I, it was shown that the soil extract after filtration through a Pasteur-Chamberland filter tube exhibited some oxidation, even when no plants were growing. It was likewise shown by the results in Table II that certain nutrient salts dissolved in distilled water were able to accomplish a material amount of oxidation without the presence of growing plants. It seems unlikely, therefore, that any considerable amount of oxidation was performed by microorganisms. If we consider the result in this last experiment, where oxidation was increased in the residue from distillation after continued boiling, it seems that any extensive action, not only of microorganisms, but also of enzymes, must be precluded. In the soil, however, it is quite probable that both of these oxidizing factors would come into play, but it is quite certain that the oxidizing power of the roots would accomplish a considerable portion of the oxidation observed.

THE NATURE AND ACTIVITIES OF THE OXIDIZING ENZYMES

Mention has been made in preceding pages of the enzymotic nature of the oxidizing action of the roots and consideration will now be given to the nature of the enzyme or enzymes which bring about the oxidation. So far as known, the oxidation effects observed were entirely due to the action of enzymes and not to the other activities connected with the growth of the roots themselves.

When a few drops of alcoholic guaiac are added to water, or a suitable solution of salts, in which wheat seedlings have grown for several days, there is sometimes a faint blue color, indicating the presence of oxidase, but more often there is no blue color. When a drop of hydrogen peroxid is added, however, the liquid turns blue, giving a color varying from medium to very intense, depending somewhat upon the age of the seedlings, and the number of roots which have grown in the culture. The guaiac-peroxid reaction indicating a peroxidase is confirmed by the reaction to phenolphthalin and aloin, both of which agree in showing the presence of peroxidase. When the roots of a young wheat plant are immersed in an alcoholic guaiac solution, they immediately turn blue, indicating that they are relatively rich in oxidase, although but little oxidase appears in the water in which they grew. This may be due to the retention of oxidase by the root cells during life, but when the outer cells are killed by the alcoholic guaiac the oxidase escapes and becomes evident through its reaction with guaiac. An aqueous extract of crushed roots, shows strong oxidase reaction as well as peroxidase reaction. In the course of a brief examination of different parts of the young wheat plants, it was found that the partially depleted seeds showed a very strong oxidase reaction when guaiac was used, while the peroxidase reaction was relatively less than in the extract of crushed roots.

When the solution in which wheat roots have been grown for some days is boiled for five or ten minutes, and cooled, the oxidase and peroxidase reactions disappear.

The temperature at which the peroxidase is destroyed was determined by heating a culture liquid which showed an active peroxidase action. The culture liquid was heated to successively higher temperatures and held at each for five minute periods. The temperature at which the enzymes appeared to be destroyed was 60° C. or very close thereto.

The culture liquid was examined for enzymes in a series of cultures of different ages to learn whether the enzyme reaction was equally strong in all. Wheat seeds were germinated on perforated cork plates floating on the surface of water in crystallizing dishes of 500^{cc} capacity. When cultures were on hand aged two, three, four, five, six, and seven days respectively, tests were made with guaiac, alcoholic aloin, and phenolphthalin.

The tests with guaiac showed that the oxidase reaction which was weak in the two- and three-day cultures was quite strong at four days. The tests with alcoholic aloin and phenolphthalin showed that the peroxidase reaction was strongest in the six- and four-day cultures, and considerably weaker in each of the others.

Certain phenomena observed in connection with the use of aloin in aqueous and alcoholic solutions, suggested that they react differently with oxidases and peroxidases. Experiments were accordingly installed to test specifically the action of each solution. Two solutions of aloin were prepared: I, 0.250^{gm} of aloin in 50^{cc} of water; II, 0.250^{gm} of aloin in 50^{cc} of 95 per cent. alcohol. One cubic centimeter of aloin solution I or II was added to 5^{cc} of liquid in test tubes, according to the plan shown in Table VIII. The tubes were prepared and aloin added at 2.45 P. M., on January 10, and the observations recorded in the third column of the table were made at 11 A. M. on January 11. The culture liquid when added to the tubes showed no oxidase but good peroxidase reaction with guaiac.

TABLE VIII

Comparative reaction of aqueous and alcoholic solutions of aloin to a liquid containing peroxidase.

Nos.	Solution	Color observed 11 A. M., January 11
1 and 2..........	Unboiled liquid + 1^{cc} aqueous aloin	pink
3 and 4..........	Boiled “ + “ “	pink
5 and 6..........	Distilled water + “ “	faint pink
7 and 8..........	Unboiled liquid + alcoholic “	deep pink
9 and 10..........	Boiled “ + “ “	yellow
11 and 12..........	Distilled water + “ “	yellow

An inspection of these results shows that when only peroxidase is present, aqueous aloin is not particularly applicable for demonstrating the presence of that enzyme in the absence of growing plants, since there was the same development of pink color in the boiled as in unboiled liquid. Alcoholic aloin, on the contrary, was changed to a deep pink in the unboiled liquid, but remained unchanged alike in the boiled liquid and in the distilled water.

The action of the different aloin solutions was next tested in liquids which also possessed a strong oxidase reaction. The roots of 10 wheat seedlings 12 days old were removed and crushed in a mortar with distilled water. The filtered liquid obtained from this source gave a strong reaction for oxidase when tested with guaiac. As before, 1^{cc} of aloin solution I or II was added to 5^{cc} of the root extract in test tubes, according to the plan in Table IX. The tubes were prepared and aloin added at 4.30 P. M. on January 13, and the observations recorded in the third column of the table were made at 11 A. M. on the following day.

TABLE IX

Comparative reaction of aqueous and alcoholic solutions of aloin to a liquid containing oxidase.

Nos.	Solution	Color observed 11 A. M., January 14
1-2-3	Root extract + 1^{cc} aqueous aloin	red
4-5	Distilled water + 1^{cc} aqueous aloin	faint pink
6-7-8	Root extract + 1^{cc} alcoholic aloin	pronounced pink
9-10	Distilled water + 1^{cc} alcoholic aloin	faint pink

The results of these experiments supplement those of the foregoing in which a peroxidase liquid was used, by demonstrating that the oxidase caused a much greater conversion of aloin to "aloin red" with the aqueous than with the alcoholic solutions of aloin. There was in the root extract a distinct peroxidase reaction to guaiac, in addition to the oxidase reaction, and it is therefore only natural that in tubes 6, 7, and 8 there should be some development of color when alcoholic aloin was added.

It is evident, from the above results, that in the absence of living plant roots aqueous aloin is principally a reagent for oxidase and alcoholic aloin for peroxidase. In the experiments where plants are employed it is however needless to say that only aqueous solutions of aloin can be used.

Aloin and phenolphthalin having shown their usefulness as indicators of enzyme action, several other substances were investigated for comparison. Leuco-rosolic acid was prepared by reducing rosolic acid with zinc dust in alkaline solution. When reduction was practically complete, the solution was filtered and neutralized with hydrochloric acid, then rendered slightly alkaline with sodium hydroxid. One cubic centimeter of this solution was added to three different liquids: I, liquid from culture 6 days old; II, the same liquid after having been boiled 10 minutes; III, distilled water. When examined 24 hours later I was pronounced rose-red, while II and III were merely faint pink; which indicates that leuco-rosolic acid is capable of showing the action of those oxidizing enzymes.

Attempts were made to use ferrous ammonium sulfate and potassium iodid as indicators of the oxidizing powers of plants by putting small amounts into cultures containing living plants. Ferrous ammonium sulfate was, in the space of time of the experiment, oxidized by mere contact with the atmospheric oxygen, and was therefore discarded as an indicator. Potassium iodid was not oxidized to free iodin, as RACIBORSKI has also found.[33]

EFFECT OF DIFFERENT CONDITIONS IN THE SOLUTIONS UPON THE ACTIVITY OF THE ENZYMES

Mention has previously been made of instances where the variation in oxidation appeared to be partly due to the acidity or alkalinity of the solution used as a culture liquid. In such cases the growth of the plant roots was affected whenever the alkalinity or acidity was very pronounced. The effect is the more harmful when young seedlings are put into such solutions, because at the beginning of the experiment, when the plants are very tender, the acidity or alkalinity is greatest and gradually diminishes during the progress of the experiment. In investigating the effect of acid or alkaline conditions in the culture media, instead of using either alkaline or acid solutions at the start, a method was used whereby the originally neutral solutions became acid or alkaline as a result of the selective absorption of the plant in withdrawing nutrients from the solution.[34] It has been demonstrated by KOHN and CZAPEK[35] that fungi may render their culture media alkaline or acid as a result of their selective absorption, whereby an acid or a basic radical is removed more rapidly than the radical to which it is linked. REED[36] has observed a similar action for the higher plants and pointed out its bearing upon the composition of nutrient solutions.

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[33] Bull. Acad. Sci. Cracovie **1905**:668.

[34] See CAMERON, Rept. U. S. Dept. Agr. **71**:67. 1902; Bur. Soils, U. S. Dept. Agric. Bulls. 30 and 41. 1905.

[35] Beitr. Chem. Phys. Path. **8**:302. 1906.

[36] Annals of Botany **21**:501. 1907.

Solutions were made up from salts whose radicals are differently absorbed by growing plants, e. g., calcium nitrate and potassium sulfate. Where calcium nitrate is furnished the plant takes up NO_3 more rapidly than Ca, with the result that the solution becomes increasingly alkaline. In the case of potassium sulfate, the plants take up K more rapidly than SO_4, with the result that the solution becomes acid. In the experiments which were made upon this problem, an attempt was made to determine the acidity or alkalinity of the solutions when the experiment was terminated. A measured quantity of solution was boiled in a platinum vessel to drive off CO_2, and then titrated. The results of these determinations are shown with the other results in Table X.

TABLE X

Oxidation and growth of wheat plants in solutions which became acid or alkaline as the result of plant growth. Relative growth measured by transpiration.

No.	Solution	Relative growth	Acidity at termination of the experiment	Alkalinity at termination of the experiment	Relative oxidation
1.......	Control in distilled water	100	.....	.....	100
2.......	30 p.p.m. Ca as $Ca(NO_3)_2$	174	.....	$n/5000$	401
3.......	30 p.p.m. Ca as $CaCl_2$	112	.....	$n/7500$	107
4.......	30 p.p.m. Ca as $CaCO_3$	123	.....	$n/7500$	175
5.......	66 p.p.m. SO_4 as $(NH_4)_2SO_4$	46	$n/7500$	.....	102
6.......	66 p.p.m. SO_4 as K_2SO_4	78	$n/10000$	.....	100
7.......	100 p.p.m. NO_3 as $NaNO_3$	201	.....	$n/5000$	401
8.......	35 p.p.m. K as KCl	92	Neutral	Neutral	97
9.......	100 p.p.m. NO_3 as $NaNO_3$ $n/620$ 63 p.p.m. K as KCl $n/620$	283	.....	$n/10000$	638
10.......	100 p.p.m. NO_3 } as KNO_3 $n/620$ 63 p.p.m. K } 63 p.p.m. K as K_2HPO_4 $n/620$	295	.....	$n/20000$	250

These results show that six of the nine solutions became alkaline, two became acid, and one remained neutral. Growth and oxidation were less in the acid solutions than in those which became alkaline, although in the case of calcium chlorid the result was quite low. In the case of potassium sulfate and potassium chlorid a part of the depression may be due to the effect of the potassium, which usually fails to increase oxidation materially, but such is not the case with ammonium sulfate. Neither is it probable that the sulfate radical is the depressing factor, since calcium sulfate compares favorably with calcium nitrate in its effect upon oxidation. The more favorable effect of no. 2 in Table X upon oxidation over nos. 3 and 4 is probably to be attributed to the presence of nitrate, which likewise appears to be responsible for a material increase in growth.

The greater oxidation accomplished by no. 9 over no. 10 is probably not to be attributed to the presence of Cl, but to the smaller amount of K present in no. 9.

On the whole it appears that while oxidation is affected to a certain extent by conditions of acidity or alkalinity arising in the culture medium, it is more materially affected by the specific action of the salts and their elements in the solution.

The direct effect of acid and alkaline conditions upon the activity of peroxidase was investigated by the following experiment in which alcoholic aloin was used as the indicator. A liquid showing strong peroxidase action was taken from a pan in which several hundred 7-day-old wheat seedlings were growing. Various amounts of *n*/50 HCl and *n*/50 NaOH were added to a set of tubes each containing 10^{cc} of the culture liquid and 1^{cc} of alcoholic aloin solution added at 3 P.M., January 13. The following table shows the amount of acid or alkali added in each tube, and gives the record of the colors observed at 11 A.M. the following day.

TABLE XI

Effect of acid and alkaline conditions upon the activity of peroxidase in the absence of plants.

No.	Solution	Color observed at end of 20 hours
1	10^{cc} culture liquid $+0.1^{cc}$ *n*/50 HCl	faint pink
2	" " " +0.2 " "	" "
3	" " " +0.5 " "	no change
4	" " " +0.7 " "	" "
5	" " " +1.0 " "	" "
6	" " " +0.1 *n*/50 NaOH	red
7	" " " +0.2 " "	wine-red
8	" " " +0.5 " "	deep wine-red
9	" " " +0.7 " "	" " "
10	" " " +1.0 " "	" " "
11	" " " neutral to litmus solution	deep pink
12	" " " " " " "	" "

From these results it can only be concluded that a slightly alkaline medium is most favorable for this peroxidase reaction. It will be remembered that WOLLNY[37] found also that the oxidation processes in the soil were distinctly favored by slightly alkaline conditions.

The effect of putrefactive processes upon oxidation is another question which was briefly investigated. When a number of seedlings were placed without any support in water containing aloin (the entire root system, seed, and lower part of the plant, being thus submerged), it has been observed that the red color first produced subsequently disappeared. An experiment was accordingly planned to learn whether oxidation phenomena would be affected when the seeds were submerged and gave rise to products of putrefaction. Twelve cultures of wheat plants were prepared and allowed to grow four days in tap water. In one-third of the cultures the seedlings were adjusted in the notched corks so that only the root systems of the plants were submerged; in one-third of the cultures the seedlings were lowered so that the seeds also were submerged, and one-third had the seedlings entirely submerged. On the fourth day 100^{mg} of aloin were added to each culture jar, and they were examined twenty-four hours later with reference to the production of colors. It was found that the cultures planted with only the root systems submerged showed a very considerable amount of oxidation, but in those where the seeds or entire plants were submerged there was none of the red color produced by oxidation. In these cultures where no oxidation was shown, there were putrefactive processes at work, a fact which is taken to mean that the oxidation effects are not observed when putrefactive processes occur. Whether this inhibition of oxidation is caused by the products of putrefaction or by a perverted metabolism, since the plant must function under somewhat anaerobic conditions, remains undecided.

That the oxidizing power of the plant was not destroyed is shown by the fact that by raising the seeds out of the culture water and refilling the jars with fresh tap water containing aloin, the characteristic oxidation occurred.

The foregoing experiments raised a question as to the amount of oxidation which occurs in poorly drained soils, where putrefactive processes are known to exist. In investigating this question, two crops of wheat seedlings were grown in Arlington clay loam in paraffined wire pots, giving the pots different amounts of water.

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[37] Die Zersetzung der organischen Stoffe und die Humusbildung. Heidelberg. 1898.

Lot I of the pots was kept at the optimum water content of the soil. The soil in lot II was kept saturated with water from the start, and the soil in lot III was saturated after the wheat seedlings were up. The relative green weight of the first crop of wheat plants, which grew from February 18 to March 14, was: I, 100; II, 111; III, 104. The relative weight of the second crop, grown from March 17 to April 8, was: I, 100; II, 67; III, 116. Extracts of these soils were then made and wheat plants were grown eleven days in the various extracts. At the end of that time the growth and oxidizing power of the plants in the different solutions were determined with the result shown in Table XII.

TABLE XII

Growth and oxidation in extracts of soils of varying moisture content. Growth expressed in terms of relative transpiration.

No.	Soil treatments	Relative growth	Relative oxidation
1................	Soil kept at optimum	100	100
2................	Soil kept at saturation	78	69
3................	Soil saturated after plants were up	151	11

These results show that the effects of the poor drainage conditions appear to be much more marked upon oxidation than upon growth. The soil, which was kept at optimum and only saturated after the plants had started, seemed to remain favorable to growth in the pots and in the extracts, but its extract was plainly not favorable to oxidation. In regard to the increase of growth, it should be remembered that this lot of soil was alternately very wet and dry during the course of the experiment.

EFFECT OF TOXIC COMPOUNDS UPON OXIDATION

Aside from the foregoing experiments, in which there were used extracts of soils which displayed toxic qualities toward plants, a few investigations were made upon the action of organic compounds whose toxic properties had been previously determined.

The organic compounds employed for this purpose were vanillin, cumarin, and santonin. The compounds were dissolved in distilled water and the resulting solutions used as cultures, taking care that the concentrations chosen were not so great as to be fatal to wheat plants within the duration of the experiment. Vanillin was used at the rate of 100 parts per million, cumarin 10 parts per million, and santonin in a saturated solution, which was nearly 100 parts per million. The growth of the plants, as measured by transpiration and stated in figures, taking the growth of similar plants in distilled water as 100 in each case, was: vanillin, 63; cumarin, 81; santonin, 75. After the plants had grown in their respective solutions for 12 to 14 days, 100^{mg} of aloin were added to each and the results noted on the following day. The results agreed in showing no color indications of oxidation in any of the cultures where the toxic compounds were present, although the roots growing in the control cultures in distilled water showed by the red color produced that a material amount of oxidation had been accomplished.

That the mere presence of organic materials did not inhibit the oxidation was shown by an experiment employing a solution of leucine which was slightly beneficial to the growth of wheat seedlings in solution cultures. Solutions of leucine containing 50 to 100 parts per million, producing an increase in growth over distilled water of 54 and 98 per cent. respectively, were very favorable to oxidation and produced a much deeper aloin red than the cultures in distilled water.

It can only be concluded, therefore, that the toxic organic compounds studied were deleterious to oxidation because of their toxic properties, and it appears that they were even more deleterious to oxidation than to plant growth.

The oxidizing action of the plants upon toxic organic substances is a phenomenon which has been pointed out by the authors in a previous paper[38] and will be referred to again later. The experiments presented in that paper also showed that the addition of sodium nitrate and calcium carbonate to solutions of toxic organic compounds went far toward decreasing their harmful effects, and in some cases overcame them entirely. That the organic salts and the physiological activities of the plants working together had accomplished the destruction of toxic substances, was shown by both plant growth and chemical tests. It now appears that while this destructive action of the plant upon the toxic body is going on, the oxidizing power in the presence of an excess, as it were, of toxic body is greatly reduced, and may even be entirely inhibited. The conclusion drawn from those experiments was that the plant roots are able to oxidize a certain amount of deleterious organic material, and that the presence of salts which favor oxidation increases the ameliorating action of the plant.

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[38] Jour. Amer. Chem. Soc. **30**:85. 1908.

This question was studied a little further by an experiment in which the oxidation in solutions of toxic material was observed. A solution of cumarin containing 10 parts per million, with and without the addition of fertilizer ingredients, was used as a medium for plant growth and subsequently examined for powers of oxidation. Sodium nitrate was added to one portion of the cultures at the rate of 50 parts of NO_3 per million, and calcium carbonate at the rate of 2000 parts per million was added to another portion of the cultures. Wheat plants were installed in the cultures October 7 and grew until October 17. The oxidation was estimated by means of aloin. Table XIII gives the effect of this treatment upon growth and upon the oxidation in the toxic solutions and in control solutions to which no cumarin had been added. In each case growth and oxidation of the plants in distilled water are taken as 100.

TABLE XIII

Effect of sodium nitrate and calcium carbonate on growth and oxidation in solutions of cumarin. Growth expressed in terms of relative transpiration.

No.	Solutions	Relative growth	Relative oxidation
1	Distilled water	100	100
2	" " $+NaNO_3$	196	250
3	" " $+CaCO_3$	170	166
4	Cumarin 10 p.p.m.	81	31
5	" " $+NaNO_3$	159	139
6	" " $+CaCO_3$	110	131

The results of this experiment show, in harmony with the previous ones, that the addition of these fertilizer ingredients overcame to a large extent the deleterious effect of the cumarin upon growth, each one making the cumarin solution to which it was added a better medium for growth than distilled water. An inspection of the figures expressing the relative oxidation shows, however, that the addition of these salts produced relatively greater increases in oxidation than in growth. When sodium nitrate was added to cumarin the resulting growth was twice as great as where only cumarin was present; the oxidizing power, however, was increased over fourfold. In comparison with this effect, it will be noted that the addition of sodium nitrate to distilled water likewise increased the growth twofold and increased the oxidizing powers two and a half times. It seems quite evident, therefore, that the ameliorating powers observed under the conditions of the experiment are to be referred to the increased oxidizing powers which are thereby brought about, and the consequent diminution in amount and activity of the toxic material.

It may be noted that LE RENARD[39] found that nitrates had a greater antitoxic value than other radicals when Penicillium was grown in the presence of copper.

SUMMARY

1. Roots of growing plants exhibit an extracellular oxidizing power which may be demonstrated by the use of suitable chromogens in nutrient solutions or soil extracts.

2. The oxidizing power appears to be most energetic in the region of the root where root hairs are found, and to decrease gradually in activity as that portion of the root becomes older.

3. The oxidizing power of plants grown in extracts of productive soils is greater than that of plants grown in extracts of unproductive soils.

4. Treating the soil extracts with an absorbing agent is usually beneficial to oxidation.

5. The distillate of a poor soil extract which contains volatile toxic compounds was less favorable to oxidation than the residue remaining from distillation.

6. The presence of toxic organic substances in solution was extremely deleterious to the oxidizing power of the plants. The oxidizing power of the plants, especially in the presence of nitrates, was able to alleviate the toxicity of such solutions.

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[39] Essai sur la valeur antitoxique de l'aliment complet et incomplet. Paris. 1907.

7. The process of oxidation is usually accelerated by the addition of sodium nitrate to an aqueous soil extract. The addition of other fertilizer salts also influences oxidation.

8. The process of oxidation by roots is largely, if not entirely, due to the activity of a peroxidase produced by the roots. This oxidizing enzyme is most active in neutral or slightly alkaline solutions. The activity of the enzyme may be inhibited by the presence of acid and also by the conditions in solutions where anaerobic processes occur.

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BOG TOXINS AND THEIR EFFECT UPON SOILS[1]

ALFRED DACHNOWSKI

(WITH TWO FIGURES)

In the north and in the middle west, notably in Indiana and Illinois, and to some extent in Ohio and the adjoining states, there are extensive swamp areas of vast importance to the state, some of which are called "unproductive," and generally are not cultivated. The statement is made, and there is certainly much truth in it, that these swamp lands should be naturally very rich in constituents needed for plant food. Many of these places represent deep basins of accumulated plant débris, and the drainage from hills further enriches the accumulation in the swamps. They are noted for their dense and luxuriant surface vegetation. Examples of swamp and bog areas in this vicinity show clearly that bog water contains apparently all of the constituents required for the nutrition, growth, and reproduction of a large variety of grasses, shrubs, and trees. However, from an agricultural point of view these muck and swamp lands seldom have given satisfaction, even after drainage or addition of fertilizers. Ample proof of this is seen in the reports of the various experiment stations (**7**, **8**). Thus far the remedies proposed, as a laboratory expedient, emphasize the fact that although some principles of soil fertility seem well established, and can be applied with definite results, there are yet many complex problems, the solution of which would materially enhance the economic importance of peat and swamp soils.

To the writer it has seemed probable for some time that work upon the chemistry and upon the physiological properties of peat and humus compounds must result in data valuable alike to the agriculturist, the forester, and the ecologist. Through an investigation on the cause of xerophily in bogs (**5**), there was gained supplementary evidence, of a more direct and positive sort, that the inhibiting factors of a bog are in part the presence in the soil water of injurious toxic substances. In that publication experimental data were given to show that the toxicity of bog water and of the bog-soil substratum can be corrected by various methods, and that the plants grown in solutions thus treated show not only accelerated growth and an increase in transpiration, but also an increase in the green and dry weight of organic matter.

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[1] Contribution from the Botanical Laboratory of Ohio State University, XLIII. This paper was in part read before Section G of the A.A.A.S., at the Baltimore meeting, December 29, 1908.

It is not known, as yet, whether the toxic action of bog water and bog soil is determined by the action of one constituent or by the combined action of several. The experiments so far completed have given no definite evidence that the toxins are merely specific excretions from the roots and rhizomes of bog plants. Preliminary tests, not here detailed, which were carried on in the winter of 1907, indicate that the toxicity may be due to a certain unstable body, of the nature of organic compounds excreted from the roots in the absence of O_2 and in heavy clay soils not adequately aerated. It is probably a product of imperfect oxidation and decomposition of proteins and other related substances, and it is possible that in respiration bog plants differ from other plants. Since then an excellent account has appeared by STOKLASA (**12**), in which similar results on the excretions by roots are announced. Largely, however, the toxicity of bog water seems to be due to another cause. During the changes which the accumulated plant material undergoes in the process of peat-making, there are alterations and reductions leading to gaseous and colloidal products but little known. The relative amount of these varies with the seasons, and no doubt also with the locality, but primarily it depends upon the stage in the progress of decomposition. CH_4 and H_2S, though produced in small quantities, have been found to constitute the principal gaseous products. They are especially noticeable when well-corked jars of bog water remain standing for some time. Studies on the character of the colloidal products are still in progress. The injurious products of a microflora accumulating in definite layers of the soil are, perhaps, an additional factor to be considered. Indeed, it is a serious difficulty in physiological ecology that a process must be assigned to a single category or broken up into a number of what often prove to be arbitrary categories, in order to arrive at results in any way intelligible. Too often is there a tendency to lay undue emphasis upon "average" conditions; and the more detailed responses which are due to localized influences are thus neglected. On the other hand, even though we decide experimentally which of the physical and chemical variables involved is of greater influence at a given stage, it still remains to determine how the *ensemble* of factors acts in the process which accompanies each physiographic change and serves as the functioning basis for morphological differences.

In connection with the experiments on the presence of injurious substances in bog water and bog soils, and their effect upon agricultural plants, the question arose whether the toxins which are harmful to plants in water cultures are injurious also to plants growing in soil containing them. This question has an added interest just now, because facts like those cited above give indications that the sterility of unproductive and "exhausted" agricultural soils may partly be caused by some toxic substance of a similar physiological and chemical origin. Different workers have observed that the growth of plants often gives rise to unfavorable conditions. The data obtained from various lines of experiments all go to prove that "exhaustion" cannot always be attributed to the removal of plant-nutrients from the soil by previous crops or by previous plant societies (**10**). To attempt a review of the literature on this problem would be out of place in the present paper. Suffice it to say that the results thus far obtained point strongly to the view that decreased physiological activity of plants lies rather in the toxic condition of the soil. The experimental proof is still regarded by many as furnishing negative evidence upon the problem (**6, 9**), and hence a spirit of controversy prevails in most of the writings upon this subject. However, it can no longer be questioned that the solution of this inquiry is of great importance to agriculture. It promises to throw new light upon many interrelations of soil and plants, and appears to afford a satisfactory explanation of some of the problems connected with the association and succession of plants, which on every other criterion would largely remain an enigma.

For the purpose of determining whether the toxins of bog water are harmful also to plants growing in soils containing the injurious substances, it was decided to employ first of all a soil medium as nearly non-nutrient as possible. Quartz is one of the chief and most nearly insoluble constituents of soil. It has been shown (2) that quartz is of minor importance in the adsorption and retention of hydroxids and various neutral salts; a knowledge of its action for bog water seemed, therefore, of fundamental importance. The quartz used was obtained from the Ceramics Department of the university. To free it from possible impurity it was subjected to a thorough washing. The air-dry quartz sand was first sifted through a sieve having meshes of 1^{mm}. Portions of about 250^{gm} of the sifted material were each placed in a large porcelain dish containing distilled water acidulated with HCl. It was usually the practice to boil the material for twenty minutes. After boiling, the supernatant liquid was decanted and fresh distilled water was added. A similar washing was carried out in *aqua regia* and later again in dilute KOH. The quartz was then washed repeatedly in boiling distilled water and finally dried at 100° C until ready for use.

The bog water used in these experiments was collected from the same central station on the bog island as described in the earlier paper. The solution is relatively clear, the suspended particles imparting to it a slight tinge of olive green to brown. It is very little acid to phenolphthalein, but alkaline to methyl orange.

Since no experiments had been made thus far to ascertain how much of the toxic property of bog water is removed by a given quantity of an adsorbing agent, series of ten cultures were prepared for this purpose. Seven of the cultures consisted each of 400^{cc} of bog water, to which was added sterilized quartz in quantities equivalent to the following volumes: 25, 50, 75, 100, 125, 150, and 200^{cc} respectively; that is, the quantities were chosen in volumes equal to a definite fraction of the volume of bog water used. The bog water and the quartz sand were shaken together in glass-stoppered bottles, and left standing for several days. When ready for use the liquid was decanted and placed in half-liter Mason jars, covered with black paper. Three control cultures were added, consisting respectively of untreated bog water, boiled bog water, and distilled water. The wheat seedlings used for these cultures were germinated in sawdust until 4 to 5^{cm} high. In later experiments the seedlings were germinated in quartz sand. They were then carefully washed in distilled water and transplanted to the water cultures. Never less than six seedlings were used in any experiment. It should be observed also that the seedlings were selected individuals out of a large number of plants. The corks used were previously sterilized and paraffined. Growth was measured by transpiration and the green and dry weight of plants. The cultures stood side by side in the university greenhouse in diffused light. The weekly atmometer readings varied between 176 and 186^{cc}. Below are given toxicity figures for bog water collected at two periods. Column I gives data for bog water collected September 12, 1908, nearly at the end of one of the most severe droughts that have been experienced in Ohio; the bog water for column II was brought to the laboratory October 16, soon after the first rains. The evidence derived from similar experiments with bog water collected at intervals of one month during the year is omitted, showing, as it does, considerable repetition. It should be noted, however, that the variation in the range of results for the seasons is considerable.

TABLE I

ADSORPTION OF BOG TOXINS BY QUARTZ SAND

SOLUTION	CORRESPONDING PLACE ON CURVE	TOTAL TRANSPIRATION FOR 15 DAYS, IN GRAMS	
		I. Sept. 12	II. Oct. 16
1. Distilled water 400^{cc}	A	7.50	7.50
2. Bog water 400^{cc}, untreated	B	10.26	14.90
3. Bog water 400^{cc}, boiled	B′	.....	54.22
4. Bog water $400^{cc} + 25^{cc}$ SiO_2	C	22.70	25.50
5. Bog water $400^{cc} + 50^{cc}$ SiO_2	D	.....	18.17
6. Bog water $400^{cc} + 75^{cc}$ SiO_2	E	39.28	13.83
7. Bog water $400^{cc} + 100^{cc}$ SiO_2	F	.....	13.56
8. Bog water $400^{cc} + 125^{cc}$ SiO_2	G	48.73	.....
9. Bog water $400^{cc} + 150^{cc}$ SiO_2	H	.....	12.87
10. Bog water $400^{cc} + 200^{cc}$ SiO_2	K	18.60	12.55

The results for these two dates have been plotted in *fig. 1*. The growth-rate in terms of transpiration is indicated on the axis of ordinates, and the progressive addition of quartz to bog water is shown on the axis of abscissas.

Before taking up the facts brought out in this series of experiments, another part of the investigation must be mentioned here. The foregoing observations suggested the query whether results obtained with soils of varying quality, fineness, and adsorbing surface would show that the toxic strengths of the same bog-water solution have approximately the same relation to each other irrespective of the nature of the filter used. It was intended to use types of soil ranging progressively through the weathering products from feldspars to kaolin. But the feldspars are highly alterable minerals, and the chemical products of feldspathic and granitic rock-decomposition are extremely varied (4). In the residues, however, which remain after leaching, free silica as quartz, and a number of rather indefinite substances known as clays, are the most abundant. In the present case the efficiency of the following substances, characteristic of the final residue of soil-forming rocks, and their allied substances, was tested: SiO_2 coarse; SiO_2 fine; kaolin; $CaCO_3$; SiC; and C in the form of air-dried humus. The materials were obtained through

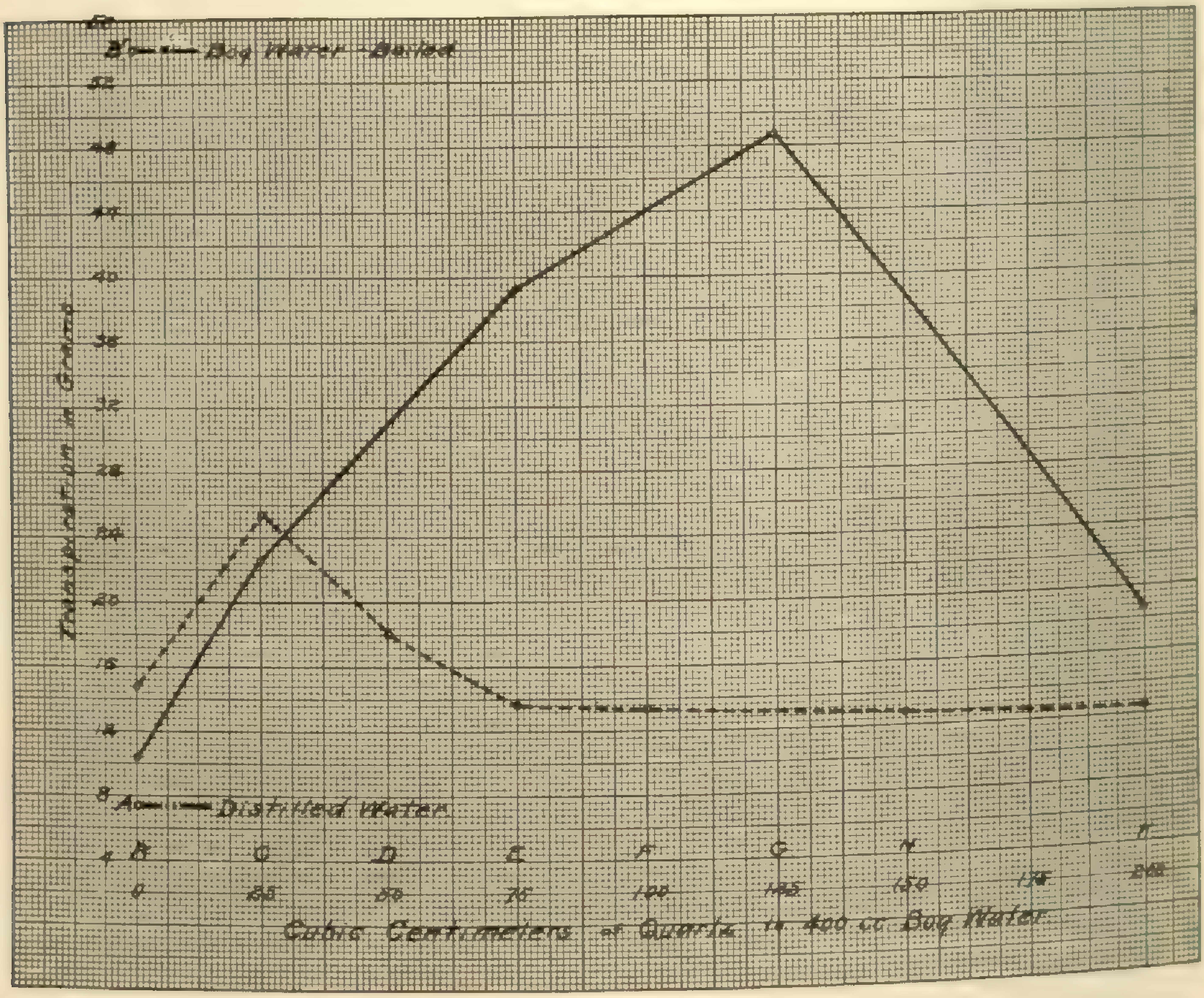

FIG. 1.—Diagram showing growth-rate of wheat seedlings in treated bog water. The ordinates represent transpiration in grams; the abscissas show the progressive addition of quartz to bog water. Unbroken lines for bog water collected September 12, 1908. Broken lines for bog water of October 16, 1908. Broken line single dotted for boiled bog water; broken line double dotted for distilled water.

the courtesy of Mr. C. H. Kerr of the Carborundum Company, Niagara Falls, New York. They are among the most insoluble substances known, and of great purity, which makes them of special value in this investigation. The chemical analysis of these materials is as follows:

TABLE II

Material	Quartz	Kaolin	Carborundum
C	.....	.....	29.71
O	.....	.....	0.45
Si	.....	.....	69.40
SiO_2	99.56	45.35	.....
Al_2O_3	0.40	38.86	0.28
CaO	.....	0.35	0.15
Fe_2O_3	.....	0.38	.....
K_2O	.....	0.61	.....
MgO	.....	0.31	0.05
Na_2O	.....	0.31	.....
Ignition	0.14	13.80	.....

The physical composition of the materials employed was determined by microscopic examination. Mechanical analysis was made with the aid of a centrifuge and for the coarser components by means of their different rates of subsidence in water. The relative percentages by weight of the different component particles in each group is as follows:

TABLE III

Material	SiO_2 coarse	SiO_2 fine	Kaolin	SiC
Sand 0.5–0.25mm	100	....	....	....
Very fine sand 0.1–0.05mm	...	6.5	2.4	79.4
Silt 0.05–0.005mm	...	80.8	61.8	16.6
Clay 0.005–0.0mm	...	12.9	35.7	4.5

To obtain the surface area of spherical particles it is only necessary to invert the value of the mean diameter of the particles for each group. This surface factor is then multiplied by the fractional amount of the quantity of the sample having particles of these mean diameters. A mathematical calculation of the surface area of quartz flour, carborundum, or other crystalline bodies with irregular surfaces, however, is not so readily obtained. It may be that adsorption of toxins and adsorption of vapors and gases are subject to the same conditions (11). Perhaps by taking measurements upon the rate of retention of a silver salt, one may secure an indirect method for the calculation of the surface of these bodies. A curve showing how the adsorption data are related to the surface presented by the grains of the different soils used, though of interest, is not a question at issue in this discussion, but it is hoped to continue this problem further, and in a more quantitative manner.

The precaution was taken to allow contact between the solution and the solid bodies for thirty minutes only, in order to reduce to a minimum the low solubility of the materials (3) and the possible action of the solution upon the solids. The amounts used in each case, and the effect of these insoluble substances on the toxic action of bog water collected January 30, 1909, are given below in Table IV. The transpiration data cover a period of fifteen days and are for six wheat plants in each solution.

TABLE IV

ADSORPTION OF BOG TOXINS BY INSOLUBLE SUBSTANCES

Solution	Transpiration in grams; six wheat seedlings in each solution			
	5th day	10th day	15th day	Total
1. Bog water 400cc, untreated	4.30	8.55	3.65	16.50
2. Bog water 400cc, filtered	4.90	10.35	6.75	22.00
3. Bog water 400cc + 15cc SiO_2 (coarse)	5.25	10.00	7.35	22.60
4. Bog water 400cc + 25cc SiO_2 (coarse)	7.20	12.85	9.80	29.85
5. Bog water 400cc + 50cc SiO_2 (coarse)	7.00	13.55	10.65	31.20
6. Bog water 400cc + 15cc SiO_2 (fine)	8.60	19.10	13.50	41.20
7. Bog water 400cc + 25cc SiO_2 (fine)	6.70	19.00	16.60	42.30
8. Bog water 400cc + 50cc SiO_2 (fine)	7.68	16.40	13.10	37.18
9. Bog water 400cc + 15cc Kaolin	9.10	20.00	16.25	45.35
10. Bog water 400cc + 25cc Kaolin	9.65	19.32	21.58	50.55
11. Bog water 400cc + 50cc Kaolin	9.95	20.10	23.40	53.45
12. Bog water 400cc + 150cc Kaolin	11.98	22.20	16.07	50.25
13. Bog water 400cc + 15cc $CaCo_3$	10.90	20.50	24.70	56.10
14. Bog water 400cc + 25cc $CaCo_3$	10.48	20.70	26.50	57.68
15. Bog water 400cc + 50cc $CaCo_3$	10.07	19.17	23.35	52.52
16. Bog water 400cc + 15cc SiC (fine)	11.23	21.25	25.60	58.08
17. Bog water 400cc + 25cc SiC (fine)	10.90	17.50*	21.20*	48.60*
18. Bog water 400cc + 50cc SiC (fine)	11.25	23.00	29.10	63.60
19. Bog water 400cc + 15cc C. (humus)	11.00	25.15	40.65	76.80
20. Bog water 400cc + 25cc C. (humus)	8.30	16.70	41.90	66.90
21. Bog water 400cc + 150cc C. (humus)	8.55	22.15	24.80	55.50

* 5 plants in culture.

Several facts seem to be clearly brought out in the above data. A comparison of the toxicity figures of bog water collected at intervals during the year indicates that the amount of toxic substances in solution differs very appreciably within the year. In all cases the physiological studies show that the adsorbing substances actually remove definite quantities of bog toxins. In contrasting the efficiency of the various amounts of adsorbents used, the important facts at the outset are these. Different physiological phases result from the progressive increase of an adsorbing substance. The bog-water solution, fatal in its effect at some seasons, gives an increase in growth-rate when adsorption removes a sufficient amount of the toxic ingredient. The effect is virtually one of dilution. Doubling of the amount of the adsorbent brings the growth-rate into a physiological phase marked by a greater functional activity. Further addition and its consequent further dilution in toxicity carries with it a corresponding intensification in growth-rate. The appearance of the plants, especially in the development of the root system, follows the transpiration figures very closely (see **5**, *figs. 1, 4–5*, p. 135). Stimulation and tolerance rise to a maximum. But with successively larger amounts of adsorbent, the optimum rate of transpiration can be neither increased nor maintained. It falls off, regularly and rapidly at first, subsequently less rapidly, until the effect of the solution is practically that of distilled water (**13**). Greater dilution and consequent increase in rate of transpiration does not express therefore the whole truth. Other and less injurious substances are also adsorbed; and the rate of transpiration is seen to be the product of a coordination of factors (**1**). In bog water with very slight toxicity, the course of the experiment shows that the maximum acceleration phase deviates very sensibly toward the growth-rate approximated in the control i.e., the untreated bog water.

On account of the difference in size of particles, there naturally follows a corresponding difference in the amount of adsorption. Compared with kaolin, calcium carbonate, carborundum, and carbon (as lampblack or humus), the adsorptive power of quartz is relatively low. It will be seen that the optimum rate of transpiration of the tenth day, in solutions 3 to 8, Table IV, is soon succeeded by a minimum. This is due to the action of toxic substances still present; for upon further addition of adsorbents the minimum at the end of the fifteenth day is succeeded by a higher rate of transpiration. Filters of finer grain are more beneficial, while the adsorptive power of humus is very much higher than that of any of the crystalline substances used. The optimum and maximum rates of transpiration occur on the fifteenth and twentieth day and lie near together. Reference to the total amount transpired shows that the adsorption of carborundum and humus is about three to four times greater than that of quartz. The transpiration data serve excellently as a basis for assigning a limit to the magnitude of the toxic effect, and as an expression of the amount of the unknown body adsorbed both in terms of the total adsorption, and as a percentage of the surface factor of grains. The results with $CaCO_3$ also show that the plants are not affected by conditions of acidity or alkalinity, and that growth seems to be more materially affected by the specific action of the organic toxins present. Whatever the nature of the filter used, that the increased tolerance of wheat seedlings to bog water is actually due to the adsorptive power of the filters is sustained by the fact that the decrease of the poisonous effects of bog water is apparently a function of surface of particles and is approximately proportionate to the quantity of the solid body used. The solution, decidedly toxic without the solid, becomes capable of supporting a more than normal growth.

The outcome of these preliminary tests is, therefore, that the conditions giving rise to decreased physiological activity, to xerophily, and to zonation of bog plants are not found in the depletion or increase of mineral nutrients in bog water, nor in a low soil temperature, but lie rather in the toxicity of the soil substratum, i. e., in the production of unfavorable soil conditions brought about by the plants themselves.

However, experiments by the water-culture method may not always be serviceable as a safe basis for argument concerning soil conditions. A number of life relations of the plant in a water culture become changed when in the soil. In what particular manner the toxic bodies are held by the adsorptive force of the filters is not clear if judged by physical or chemical analysis. The marked retention of the toxins of bog water observed may be due to causes other than a direct condensation on the surface. No experiments were made to show conclusively that the retention is not due to chemical fixation or substitution. The amount of solution thrown out of the quartz by the centrifugal machine was too small to be tested. A priori, it would seem that the filter used should be markedly more toxic now than the solution, when tested by physiological criteria. The presence of the adsorbed bodies in the solid should not only reduce its effectiveness when repeatedly used for improving bog water, but should replace normal growth by an abnormal retardation judged from the growth-rate made in a similar check soil culture.

To obtain evidence on this point, and to contrast the efficiency of the various constituents of agricultural soils for adsorption, a series of experiments was made with quartz, river sand, field clay, and humus soil. The air-dry soils were sifted through a sieve with meshes of 1^{mm}. Portions of 400^{cc} of the sifted soils were each placed in glass-stoppered jars containing 1200^{cc} of bog water. The glassware employed in all of the experiments cited was treated with a solution of potassium dichromate and sulfuric acid, and repeatedly rinsed in distilled water previous to use. The mixtures of bog water and soil were left standing in the dark room for three days. To insure thorough contact between the bog water and the soil, the solution was occasionally shaken. When ready for use the liquid was filtered off, and portions of 400^{cc} of the liquid from each soil type were used as water-culture experiments in the manner described above. For the investigation on the relative fertility of the soils used as filters, earthenware pots were used. The pots were new and each of about 300^{cc} capacity (8^{cm} in diameter, 8.5^{cm} deep). They were thoroughly cleaned and dried in an oven at 110° C, and later immersed in heated paraffin. To each paraffined pot was added 200^{cc} of the contaminated soil well pressed into the bottom and sides of the pots. It was recognized that difficulties of obtaining good contact between the soil and the walls of the pot would be probable. In the air space along the walls usually by far the greater proportion of plant roots are developed, and the wire-basket method as recommended by the Bureau of Soils of the U. S. Department of Agriculture (Bull. 23) is, therefore, more desirable. But the form of retainer here described was found to be wholly satisfactory. In no case were evidences found of roots growing more freely at the sides of the pot than in the center. The experiments were repeated later by the wire-basket method with the same results. Six wheat seedlings were transplanted in a row in the soil of each pot. In identically the same manner a series of duplicate cultures with the untreated soils was prepared to serve for comparison with the behavior of wheat seedlings in the contaminated soils. The filled pots were then weighed and placed in the greenhouse where they stood side by side. Direct sunlight was avoided by cloth screens. Only one of the experiments need be given, and Table V gives a summary of the results obtained with bog water collected September 12, 1908. The percentage increase is calculated upon the basis of the quantities marked zero (0), considering them as unity for the respective series. The photograph (*fig. 2*), which I owe to the aid of Professor J. H. SCHAFFNER, shows these plants at the end of the experiment.

TABLE V

ADSORPTION OF BOG TOXINS BY SOILS

SOLUTION	AVERAGE LENGTH IN CM.		PERCENTAGE INCREASE		
	Tops	Roots	Transpiration	Green weight	Dry weight
1. Bog water untreated........	15.8	5.3	0	0	0
2. Bog water quartz-filtered...	20.8	42.	338.	134.	56.
5. Bog water clay-filtered.....	19.9	11.4	154.	68.	11.
8. Bog water humus-filtered..	30.5	15.6	805.	220.	84.
3. Contaminated quartz soil..	22.	12.3	....	0	0
6. Contaminated clay soil....	22.2	6.6	...	0	0
9. Contaminated humus soil...	21.9	6.2	...	0	0
4. Control quartz soil.........	24.7	9.6	...	8.	20.
7. Control clay soil..........	26.	11.7	...	25.	5.
10. Control humus soil........	30.7	13.5	...	86.	55.

Again it is evident that the addition of solids has increased the tolerance of the seedlings to bog water. The improvement was marked during the entire period of experimentation. The presence of the toxic bodies in small amounts exerted a noticeable stimulating effect, while the plants in the control bog water gave every indication that they would be unable to survive an exposure of a normal growing period. The last-mentioned point has been repeatedly tested also in field-work. It seems as if the roots, and especially the more minute roothairs, of the plants in the untreated bog water served as adsorbing surfaces. The roots are brownish in color and jelly-like in consistency; deposited upon their surfaces are found numerous colored bodies, as the result of the oxidizing action of the roots. The nature of these bodies is still under investigation. A general decay of the growing tips is noticeable, showing that the oxidizing action of the plants upon the toxic substances went far toward decreasing their harmful effect, but could not entirely overcome them. The effectiveness of adding the insoluble solids proves, therefore, very conclusively that the source of the harmful condition must logically be looked for in the solution and not in the condition of the plants themselves. The difference in the tops as well as in the roots of the plants from the various cultures is very striking. The stimulation effect is less marked in the solutions filtered through clay and humus, because of the greater adsorptive power of these substances; yet the increase in the green and dry weight of plants is relatively twice that in the untreated bog water while transpiration has increased almost tenfold. The introduced materials have had their adsorptive action, but it is evident

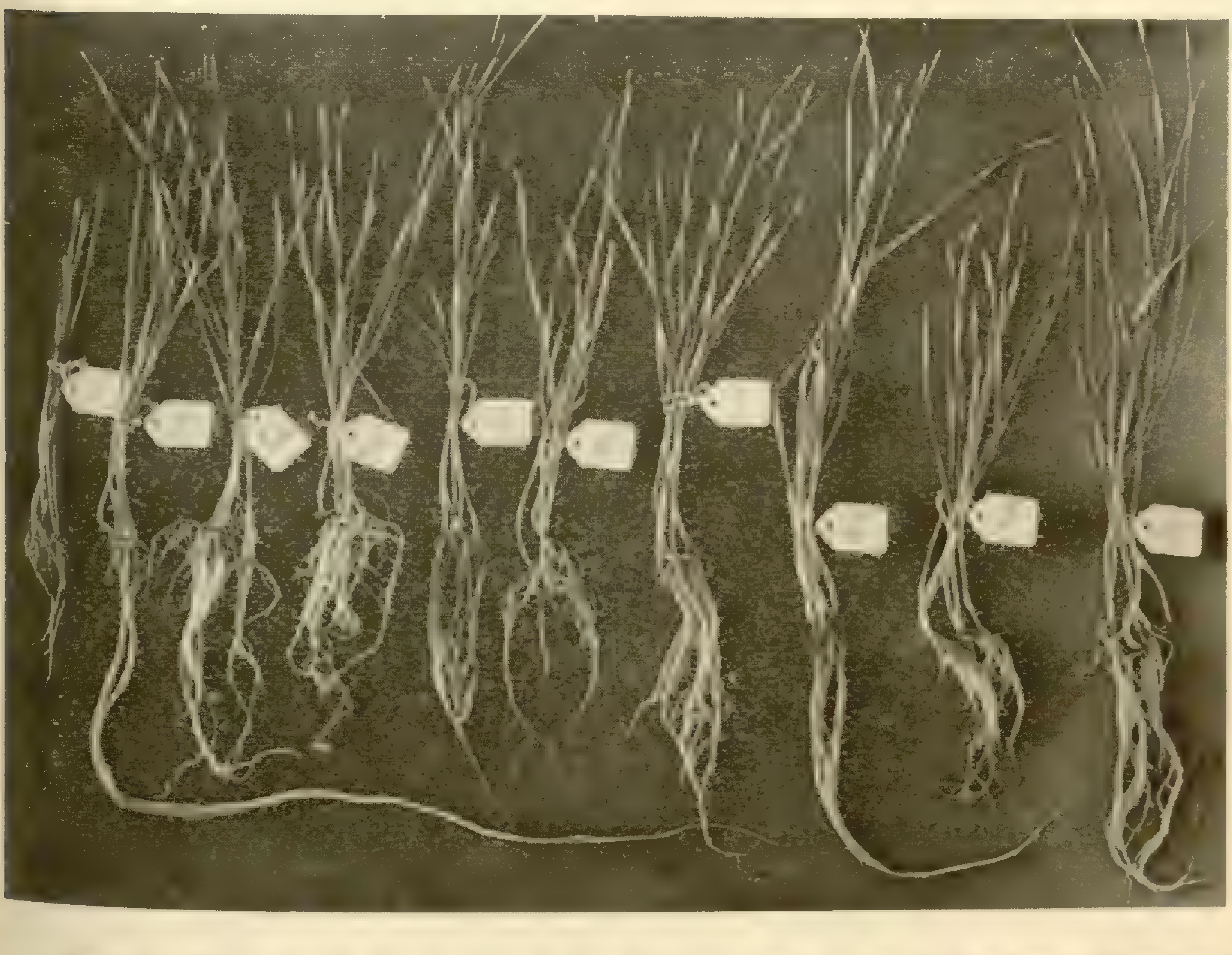

FIG. 2.—Growth of wheat plants in various cultures of bog water. Numbers as in Table V.

also that chemical reaction enters in the case of the common types of garden soil.

We come finally to a consideration of the effects of bog toxins upon soils. It is to be noted that the poisonous action of bog toxins is more harmful when the plants are immersed in the solution, than when grown in the contaminated soil cultures. That the poisonous matter injurious to plant growth is present in the soils used as filters is seen upon comparison with the controls. Manifestly, the theory of lack of O_2 in bog water or in bog soils as the cause of xerophily is not satisfactory to account for the results, because water cultures usually have less O_2 than any soil medium. The transpiration data for boiled bog water (Table I, page 393) are further evidence in this direction. The inadequacy of the theory of low substratum temperature is, for this locality, equally obvious. That the action cannot be attributed to large amounts of dissolved substances has been shown in the determination of the osmotic pressure of bog water in the author's earlier paper (*l. c.* **5**). The garden soils contain a much larger amount of nutrient ingredients than bog water, and hence the presence of those salts should tend to increase the growth-rate. No such increase in activity occurred. The length of time during which the wheat plants were allowed to grow is palpably insufficient to "exhaust" or contaminate the soils. The retardation seen in the contaminated soils is lacking the corresponding normal average in dry weight of plants to an amount of 18 per cent., 3 per cent., and 36 per cent. for quartz, clay, and humus respectively. From the results it may be concluded that the adsorption and retention capacity of soil for toxins is generally higher the greater its content of humus. It was shown elsewhere that a bog-water solution well aerated, or upon long standing with exposure to air, lost its injurious properties. When plants are grown in this oxidized solution it is found that the solution becomes decidedly beneficial to plant growth. These results are also obtained with the contaminated soils. When first used they exert a distinctly injurious effect. If the amount of water transpired by the plants is replaced by bog water, the soils become more toxic. Decrease in toxicity always follows aeration of the soil and drainage; and since the physical conditions mainly determine the amount of oxidation, these are of greater consequence in restoring the fertility to the soil.

SUMMARY

The available information of the study here reported may be summarized as follows:

1. Many swamp and muck soils exhibit a sterility which cannot be remedied by drainage or by the addition of fertilizers.

2. The sterility appears to be most marked where investigations on the physiological properties of bog water and bog soils indicate a greater amount and activity of bog toxins.

3. The production of bogs toxins is due to a number of physical and chemical factors. One can only conclude that the chemical constitution of bog water and bog soils at a given moment conditions toxicity; and that the excretion from roots and rhizomes of plants is one of the variables of the conditioning factors.

4. In untreated bog water there are found deposited upon the roots of wheat plants numerous colored bodies as the result of the oxidizing action of roots. The general decay of the root-tips indicates that the oxidizing activity is insufficient to decrease the harmful effects of bog toxins.

5. It is possible that ecesis, association, and succession of plants depends primarily upon respiration, and that in respiration bog plants differ from other plants.

6. Treating bog water with an insoluble adsorbing agent is invariably beneficial.

7. Different physiological phases result from the progressive addition of an adsorbing substance. With coarser-grained materials the low optimum rate of transpiration is soon succeeded by a minimum which is due to the action of toxic substances still present.

8. Finer-grained insoluble bodies are more beneficial. The response to toxic bodies when present in small amounts leads to acceleration of growth. The period of growth is more prolonged, and the optimum and maximum rate of transpiration lie near together.

9. The adsorptive action of carborundum and humus is about four times greater than that of quartz; the capacity of soils for retaining toxins is therefore higher the greater the content of humus.

10. The decrease of the poisonous effect of bog water is probably a function of the surface of the particles; it is relatively proportionate to the quantity of the solid body used.

11. In agricultural soils used as adsorbents the presence of the adsorbed unknown toxins replaces normal growth by an abnormal retardation. Fertility is restored through aeration, that is, after time enough has elapsed for the oxidation of the injurious bodies.

12. The contaminated condition of agricultural soils and the consequent decreased physiological activity of the plants grown in them still further indicates that xerophily cannot be due to acidity, lack of oxygen, low temperature, etc., of the soil substratum; that is, the factors heretofore cited are only in part the cause of xerophily.

In view of the evidence presented above, the writer believes that these facts in the action of bog water upon soils justify the conclusion that there are present in bog water and in bog soils injurious substances which are, at least in part, the cause of xerophily in plants, and of decreased fertility in bog soils.

Grateful acknowledgment is made to Professors McCall and Vivian, of the Agricultural College of the university, for the facilities of their laboratories, which were freely and courteously placed at the writer's disposal.

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BRIEFER ARTICLES

PARTHENOGENESIS IN *PINUS PINASTER*

(WITH SEVEN FIGURES)

In the course of an investigation on the life-history and development of the embryo of the cluster pine, *Pinus pinaster* Soland., it has occasionally been noticed that in some ovules containing proembryos in all stages of development either no trace of pollen tubes could be seen in the nucellar cap, or the tubes only extended through a part of the nucellus and no nuclei could be found in them. This strongly suggested the occurrence of parthenogenesis, but might have been due to imperfect preparations. Therefore, in 1908, collections were made about every twelve hours during the time when the archegonia mature, in the hope of obtaining more satisfactory evidence.

Great care was used in fixing and imbedding this material, and the following fixing agent has been found more satisfactory than any other, including chromacetosmic mixtures.

Picric acid, saturated solution in 50 per cent. alcohol, 100^{cc}; corrosive sublimate 5^{gm}; glacial acetic acid 5^{cc}. This fixing agent is mentioned by CHAMBERLAIN,[1] and I have to thank Mr. A. J. BALLANTINE for suggesting its use. Cedar-wood oil has been found much superior to xylol to precede the infiltration with paraffin, as mentioned by Miss FERGUSON (**'04**). The stains used have been Delafield's hematoxylin, much diluted and allowed to act for several hours, and Flemming's safranin gentian-violet orange-G combination. The first named shows nuclear details more sharply than the triple stain and is only equalled in this respect by Haidenhain's iron alum hematoxylin, which is more troublesome to use and in no way superior. In other respects the methods used have been those generally employed in cytological work.

The evidence obtained shows clearly that parthenogenesis occasionally occurs, and the most conclusive preparations are shown in *figs. 1* and *2*.

The points which seem to prove satisfactorily that the oosphere develops without fertilization taking place are as follows:

1. Although the oosphere nucleus has divided or begun to divide, the pollen tube has not yet reached the archegonium and still contains both the sperm nuclei (*figs. 1, 2*).

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[1] CHAMBERLAIN, C. J., Oogenesis in *Pinus Laricio*. BOT. GAZETTE **27**:268–280. *pls. 4–6.* 1899.

2. A careful study of the other sections of the series has failed to show any other pollen tube which might have reached the archegonium from another direction.

3. The spindle of the

EXPLANATION OF FIGURES

All sections 6–8 μ thick; cut with the Cambridge rocking microtome; drawn with camera. In all: *n*, nucellus; *p*, prothallus; *t*, pollen tube; *a*, archegonium; *v*, receptive vacuole; ♀, oosphere nucleus; ♂, functional sperm nucleus; ♂$_2$, secondary sperm nucleus.

FIGS. 1 and 2.—Stages in the first division of a parthenogenetic proembryo; diagrammatic; reconstructed from several sections in each case. ×77.

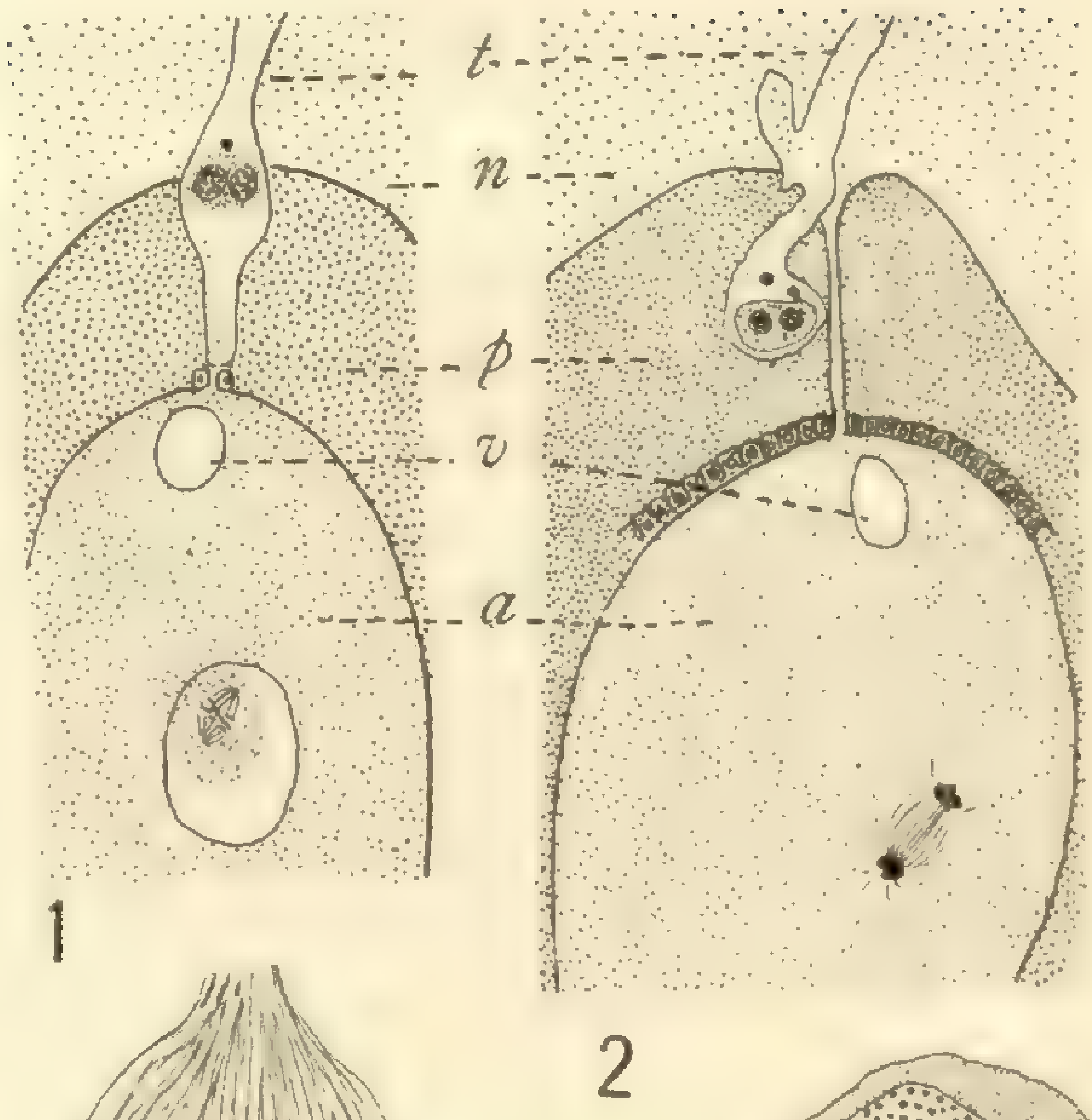
FIG. 3.—Spindle of *fig. 1*, showing the comparatively small amount of chromatin substance; drawn from two sections. (No attempt has been made to show all the chromosomes.) ×640.

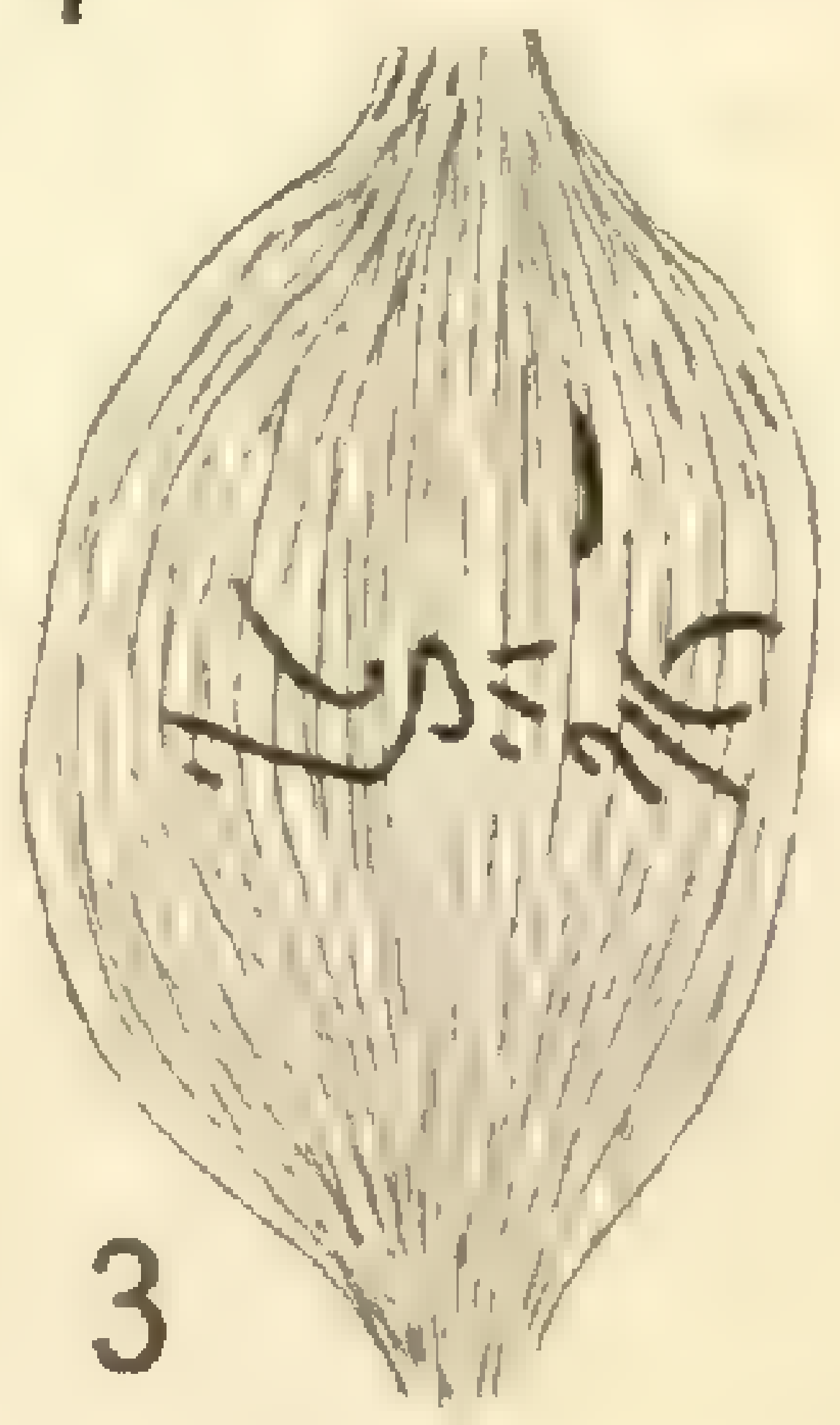
FIG. 4.—One of the sperm nuclei of *fig. 1*, showing that these are quite normally organized. ×310.

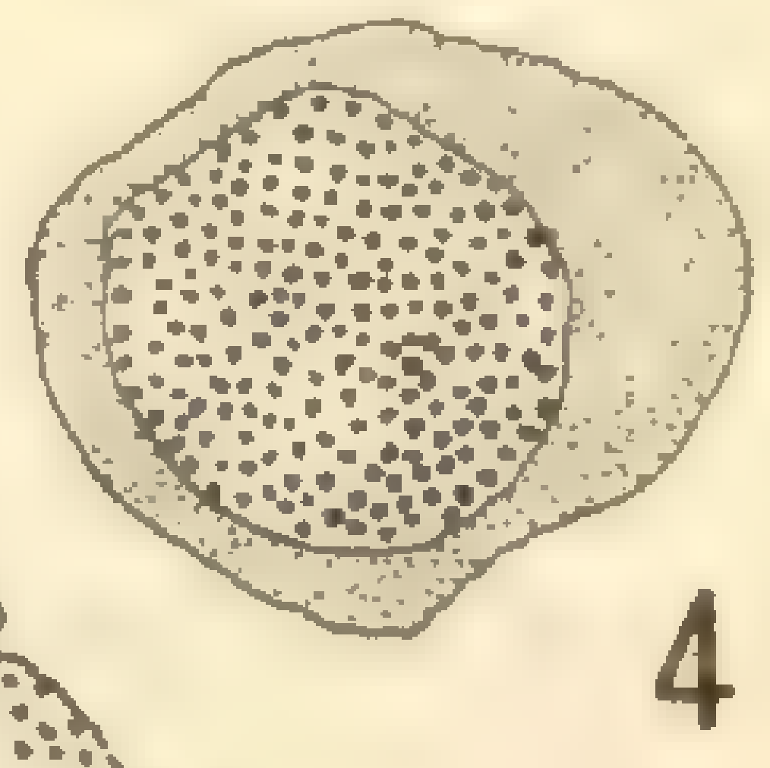
FIG. 5.—Diagram showing normal fertilization in one of the archegonia. ×60.

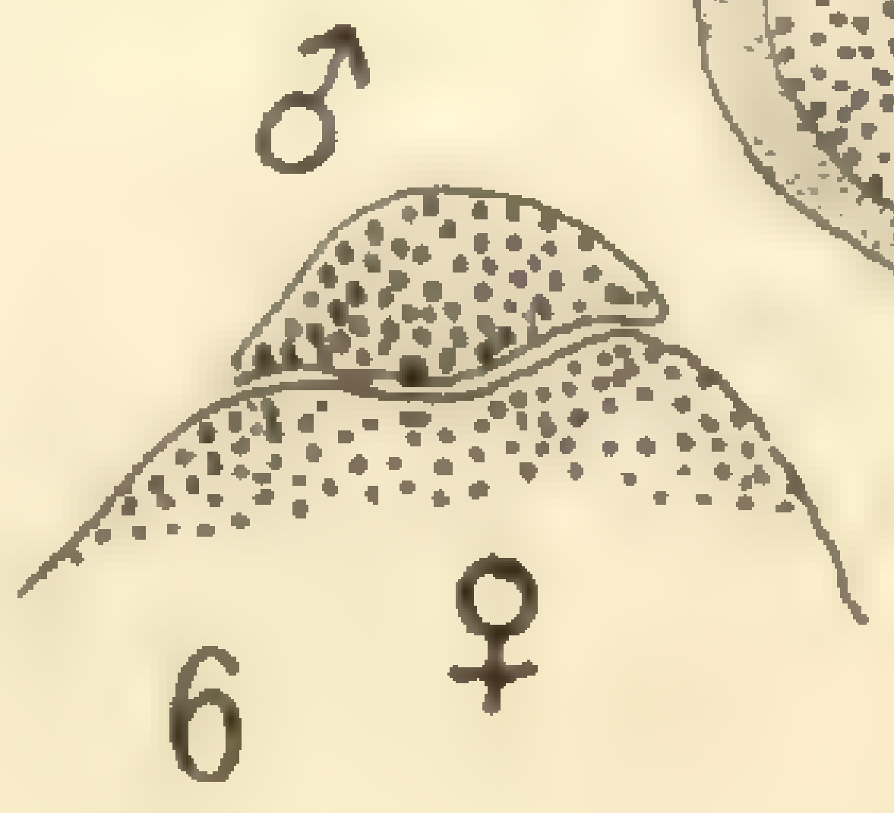
FIG. 6.—Sperm nucleus and part of the oosphere nucleus of *fig. 5*. ×255.

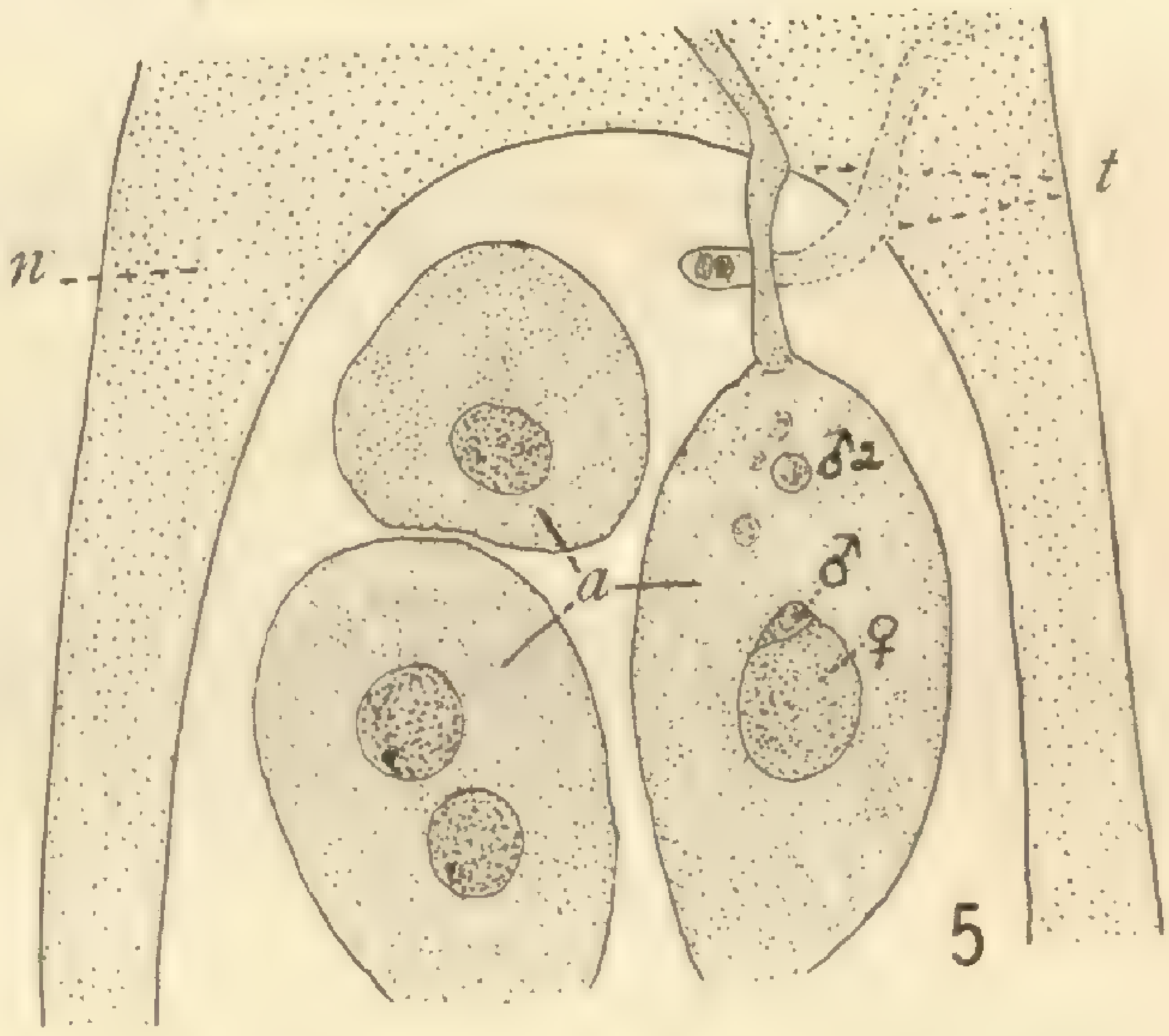
FIG. 7.—Part of *fig. 6*. ×1240.

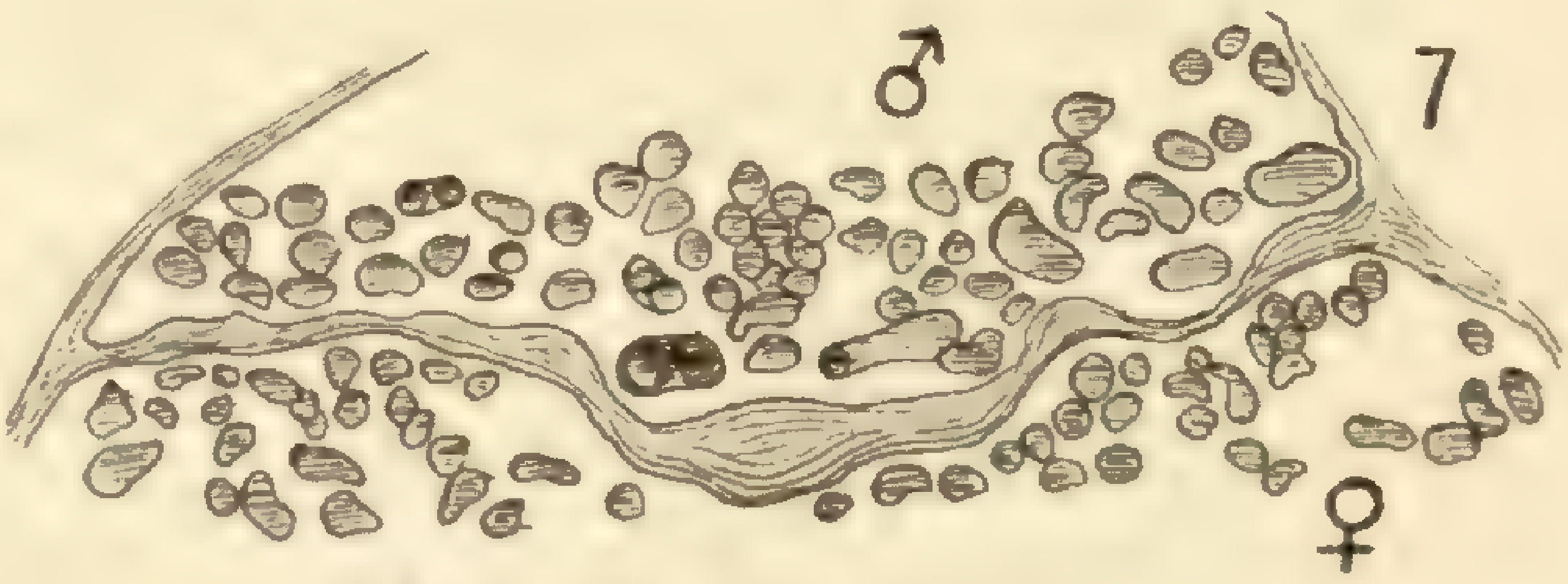












first division of the oosphere nucleus is parallel or oblique to the long axis of the ovule and is approximately in the center of the original nucleus. The normal spindle, on the other hand, is more or less transverse to the long axis of the ovule and lies quite at the top of the original oosphere nucleus. In both cases this spindle is entirely intranuclear, as shown by CHAMBERLAIN,[2] and some of the original achromatic nuclear material is not used up, but contracts considerably from the original nuclear membrane. (This contraction may be due to the action of fixing or other reagents, but as it is equally present in all preparations, whether or not any contraction has occurred elsewhere, I am inclined to think it normal.)

4. In normal fertilization a segregation of the chromosomes into two groups occurs both in the first and second divisions of the oospore nucleus, but no segregation can be seen here (*fig. 3*). The chromosomes are long and rather irregular in shape and are often cut into several pieces and distributed through as many sections. It has therefore been impossible to count them accurately, but the number in the normal sporophytic nucleus is certainly in the neighborhood of 24, and in the spindle of *fig. 3* it is as certainly less than that number.

5. In normal fertilization a good deal of disorganization of the apical part of the archegonium occurs, and the receptive vacuole is either broken or considerably displaced (*fig. 5*). In the archegonium from which *figs. 1* and *2* were drawn, no such disorganization has occurred, and the receptive vacuole occupies its normal position.

6. In normal fertilization the remains of the second sperm nucleus and the tube nucleus and the stalk cell can be distinguished for a time in the upper part of the archegonium, but no trace of these nuclei can be found in the archegonia of *figs. 1* and *2*.

As far as has been seen, the abortion of the ovule frequently occurs before the formation of a proembryo, but never after. A large number of preparations of the proembryos and embryo in all stages of development leaves no doubt on this point. Hence it appears that parthenogenetic embryos must develop as well as normal ones. It is impossible to say whether this development is only intraseminal, or whether seeds containing such embryos are able to germinate and produce normal plants.

Fig. 5 shows, for the sake of comparison, a case of normal fertilization, and the conjugating nuclei are shown in more detail in *figs. 6* and *7*. The preparation shows very clearly that the nuclear membranes are not in contact, but separated by a thin layer of cytoplasm, as mentioned by Miss Ferguson.[3]

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[2] CHAMBERLAIN, C. J., Methods in plant histology. Second edition. The University of Chicago Press. 1905.

In *fig. 5* the second pollen tube is evidently on its way to the smallest of the three archegonia, and is taking its way laterally through the tissue of the prothallus instead of down the canal leading to the neck.

The third archegonium is apparently sunken in the tissues of the prothallus, but unfortunately the series is incomplete, and it may have only a very obliquely placed neck. For the same reason it is impossible to say whether this proembryo is really parthenogenetic, as it appears to be.—W. T. Saxton, *South African College, Cape Town.*

CARNATION ALTERNARIOSE[4]

(WITH EIGHT FIGURES)

To a leaf-and-stem disease of the cultivated carnation, *Dianthus Caryophyllus* L., our attention was called by local florists as causing serious damage. The disease, upon examination, proved to be one hitherto undescribed and a laboratory study of it was undertaken.[5]

Symptoms.—The disease manifests itself as spots, mostly upon the leaves, sometimes upon the stems, especially at the nodes. These spots are strikingly characteristic, of ashen whiteness, with the center occupied by an often scanty, though sometimes profuse, black fungous growth. The diseased spot is dry, somewhat shrunken, thinner than healthy portions of the leaf, approximately circular, though often somewhat elongated in the direction of the longitudinal axis of the leaf (*fig. 1*). When occurring at the node, the disease usually involves the bases of both of the leaves, as well as the stem between them (*fig. 2*). As these nodal spots age, the disease penetrates through the stem, killing its tissue, which shrinks some-

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[3] Ferguson, M. C., Contributions to the knowledge of the life-history of Pinus, with special reference to sporogenesis, the development of the gametophytes and fertilization. Proc. Washington Acad. Sci. **6**:1–202. *pls. 1–24.* 1904.

[4] This termination was suggested by the authors in Annales Mycologici **7**:49. 1909, with the following explanation: "We believe that much will be gained both in clearness and brevity by designating diseases in plants by the uniform termination 'ose' (Lat. *osus*, signifying 'full of') added as a suffix to the genus of the causal fungus, with or without elision of the ultimate syllable of the generic name, in whole or in part, as may be determined by euphony."

[5] Through the kindness of Dr. W. A. Orton of the U. S. Department of Agriculture, B. P. I., we learn that a Macrosporium disease of carnation was reported from Strassburg, Pa., in 1906, and one attributed to Alternaria from Connecticut by Clinton in the same year.

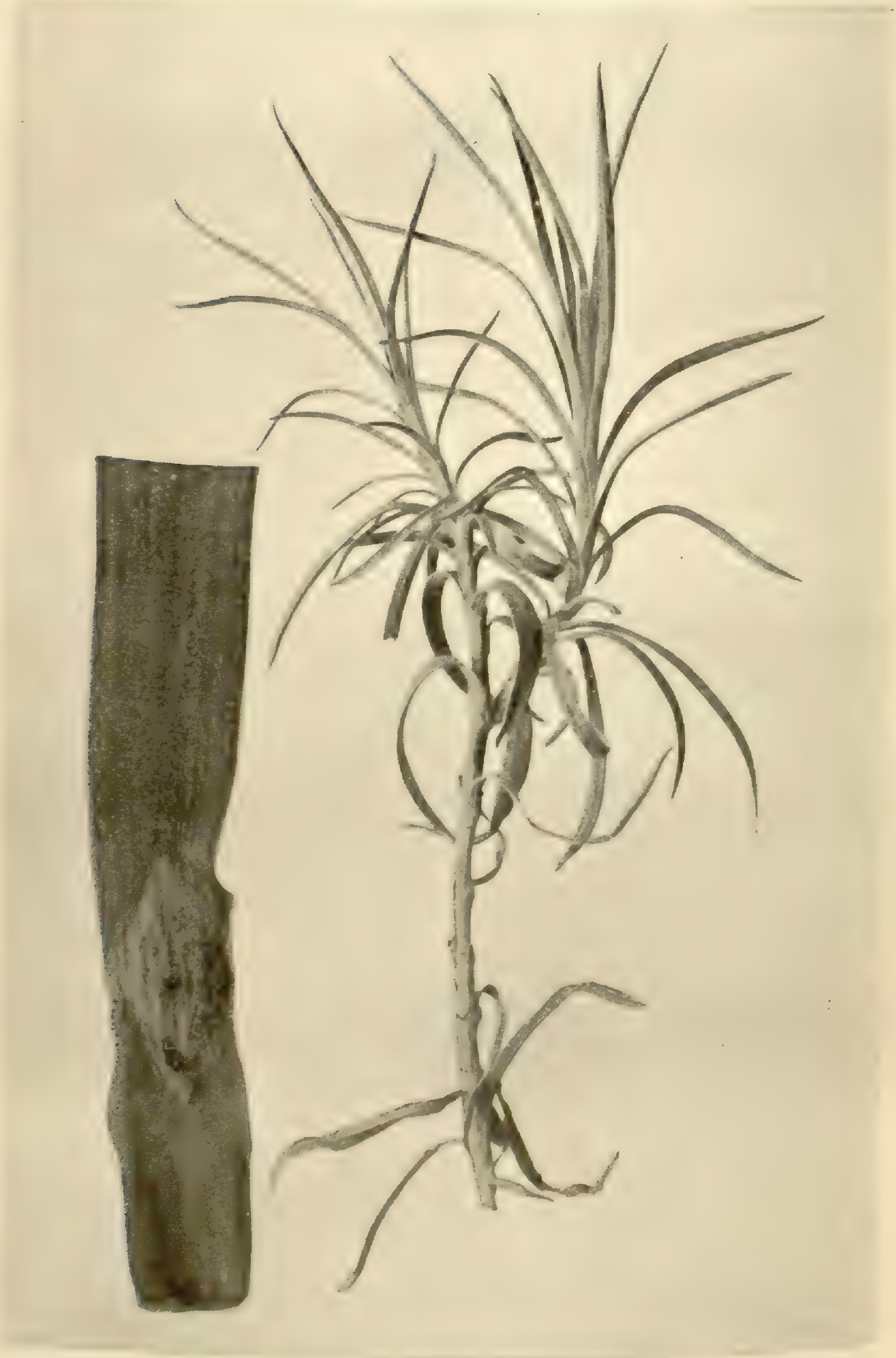

FIG. 1. Single leaf showing diseased spot near base.—FIG. 2. Diseased plant showing removal of lower leaves by the gardener in his efforts to stop the progress of the disease.

what and becomes soft and disintegrated, resulting in the death of the more distal portions of the plant.

Variety of carnations affected.—A striking feature of this disease is its tendency to infect to a large degree one variety, the Mrs. Thomas W. Lawson, to the exemption of others. In all cases which have come to our notice, it has been this variety solely which was diseased; moreover, the only records that we find of the disease imply the same susceptibility.[6]

The causal fungus.—Throughout the diseased tissue of all spots occurs in great abundance a characteristic, dark, branching, septate mycelium (*fig. 3*). The surfaces of diseased spots in periods later than their earliest youth present an abundance of black cespitose hyphae arising from the stomata (*fig. 4*). Spores of the Alternaria type are found in abundance (*figs. 5, 6*), both *in situ* upon these hyphae, and strewn over the surface of the diseased spots between the hyphal bases. The character and arrangement of the hyphae are shown in *figs. 7* and *8*. This fungus was constantly associated with the disease, and no other fungus was found. The presumptive evidence was therefore very strong that this fungus was the cause of the disease. In view of the often saprophytic habit of Alternaria, conclusions on this point would not be valid without evidence from inoculations.

Inoculations.—The fungus was easily isolated by direct transfer of spores from the diseased spots to carnation-leaf agar plates.

On October 27 numerous inoculations were made upon two plants under bell jars, using small pieces of agar, bearing spores and mycelium. One of the plants was left uninjured and the inoculum was placed in the axils of the leaves; in the majority of these cases the inoculations resulted in infection. The other plant was injured by the prick of a needle at the point of inoculation. In these cases about two-thirds of the inoculations were successful. Inoculations with spore suspension were also made upon five branches each, of two other plants, and each was covered by a large test-tube plugged around the stem with cotton to preserve a humid atmosphere. As in the former cases, the inoculations on one plant were at injured points, and those on the other plant were at uninjured points. The results from these spore inoculations were the same as in the cases of inoculations with agar blocks. When these inoculations were made, others were made upon six other plants from the same spore suspensions, but the plants were not covered or injured in any way. Following these last inoculations no signs of the disease were seen. It seems from these experiments that the injured plant is readily susceptible to infection, as is also the uninjured plant if kept in humid condition, but that the uninjured plant in a relatively dry atmosphere is difficult or impossible to infect. In case of successful inoculation, the diseased spots were well developed at the end of a week. The removal of the protecting bell jar from plants already infected resulted usually in cessation of development of the spot. These facts agree well with the field observation that the most damaging infection occurs at the leaf axils, points well adapted to collect and hold water, thus providing conditions for optimum development of the fungus.

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[6] ORTON, W. A., Yearbook, U. S. Dept. Agric. **1905**:611.

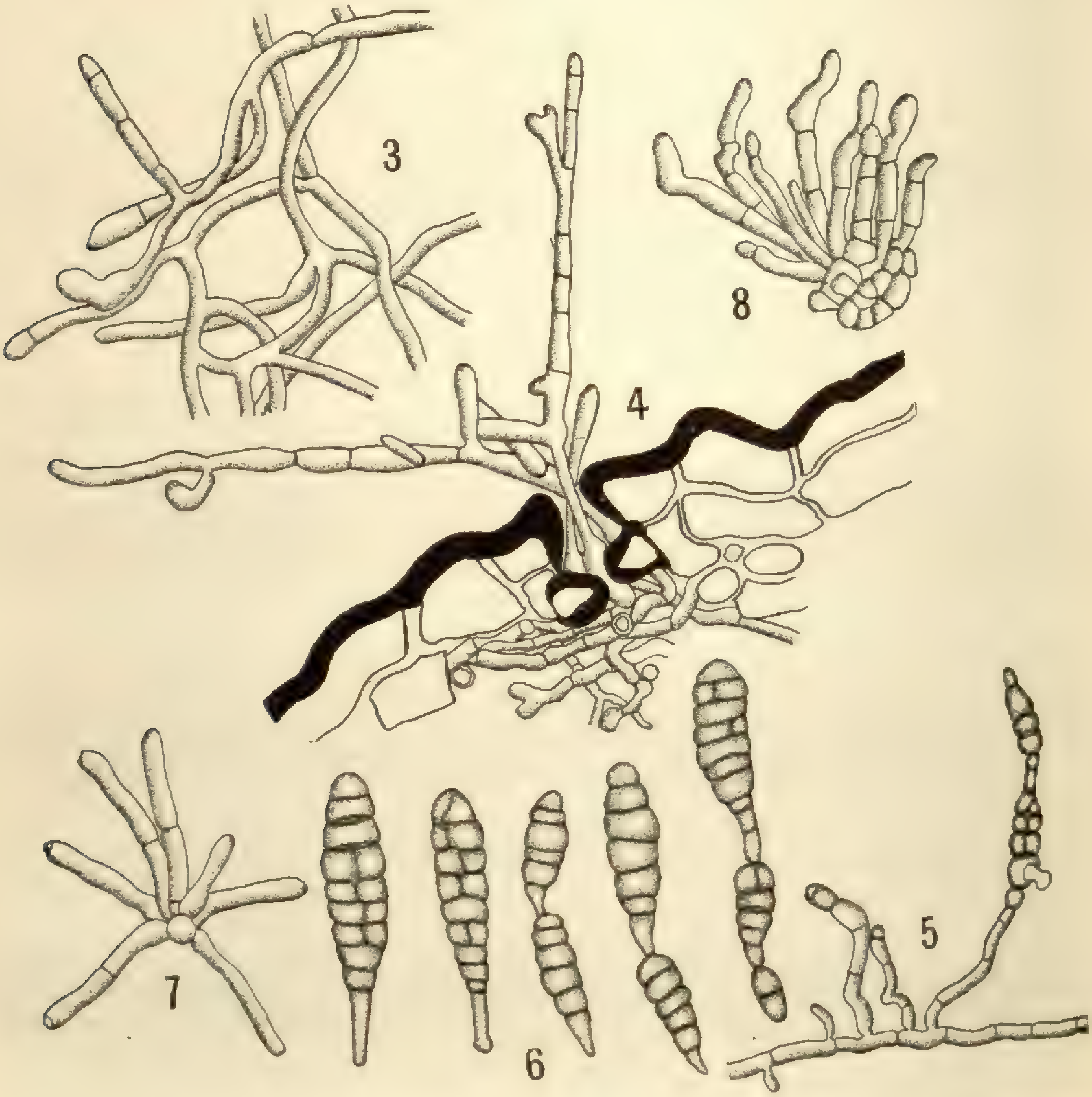

FIG. 3. Mycelium showing branching and septation.—FIG. 4. Showing mycelium below stoma and hyphae emerging through the stoma.—FIG. 5. Showing catenulate spores as borne upon hyphae.—FIG. 6. Spores showing shape, septation and catenulation.—FIG. 7. A young cluster of hyphae.—FIG. 8. An older cluster of hyphae.

Culture characters.—The fungus was grown upon many different media. Its characters upon these media have been noted elsewhere.[7]

The most important culture characters may be summarized as follows:

Upon media poor in available carbohydrates the mycelium was nearly hyaline, and the hyphae and spores pale; upon media rich in carbohydrates the mycelium, hyphae, and spores were very dark. Upon the natural medium the spores were more regular and uniform in shape and were much larger than upon artificial media.

The species of fungus.—Of the Alternarias there seems to be only one, *A. longispora* McAlph., growing upon members of the pink family (Caryophyllaceae),[8] and the description of this does not agree with ours in size, shape, or septation of its spores.

Therefore, unless an attempt be made to identify this form with some one of the seven or more species of Macrosporium infecting the pink family, a procedure which would be unjustifiable without resort to cross-culture inoculations and extensive study in artificial media, this form had best be designated as a distinct species, for which we propose the following name and description:

Alternaria Dianthi, n. sp.—Hyphae cespitose from stomata, amphigenous, dark brown, 1–4-septate, ascending, 1–25 from each stoma; conidia 26–123×10–20 μ, catenulate, clavate, tapering, base obtuse, dark brown, slightly constricted at the septa, transverse septa 5–9, longitudinal septa 0–5; spot ashen white, definite, subcircular.

On artificial media poor in carbohydrates mycelium lighter in color, spores lighter, smaller, and with fewer septa.

HABITAT: living leaves and stems of *Dianthus Caryophyllus*, Raleigh, N. C.—F. L. STEVENS AND J. G. HALL, *N. C. Agricultural Experiment Station, West Raleigh.*

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[7] STEVENS AND HALL, Variation of fungi due to environment, *ined.* Read before the Botanical Society of America at the Baltimore meeting, December, 1908.

[8] SACCARDO, Syll. Fung. **18**:638.

CURRENT LITERATURE

BOOK REVIEWS

Another mushroom book

Mushrooms, by reason of their beauty and edibility, are almost as attractive and popular as pretty wild flowers, and so we may expect to see popular guides to their collection and consumption multiply. The latest candidate for favor is a book by Mr. HARD, now superintendent of public instruction in Kirkwood, Mo., but for some years located in southern Ohio, where he became interested in collecting and studying these plants. Under the encouragement of KELLERMAN, ATKINSON, LLOYD, MORGAN, PECK, and other mycologists, he has evidently become an enthusiastic amateur. By his camera, supplemented occasionally by those of his friends, he has pictured a great number of representative specimens. Presenting these photographs, to the number of 500 and more, combined with descriptions, sometimes technical, but usually popular and more or less diffuse, he has prepared a ponderous volume.[1]

This volume, chiefly on account of its excellent half-tone illustrations, which include almost all of the common species, will be of good service to those who wish a book less expensive and voluminous than MCILVAINE'S, and at the same time comprehensive enough to enable them to identify the plants they pick up in fields and woods.

It is evident that the author has no adequate technical training in taxonomy or morphology; and in presenting such matters, neither his keen powers of observation nor his enthusiasm could prevent him from falling into errors both of form and fact. The typography of the book shows, also, that both author and publisher are unacquainted with scientific practice, while the proofreader and the author alike are responsible for many typographical errors. The etymology of the scientific names, by which the author hopes to show their significance to those unaccustomed to them, is often erroneous and occasionally ludicrous. The glossary does not define all the technical terms that are used, no less than four in a single description of eight or ten lines having been hit upon by mere chance. The list given of authorities for generic and specific names is far from complete, so that abbreviations used in the body of the text (which are not consistent) could not possibly be identified.

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[1] HARD, M. E., The mushroom, edible and otherwise; its habitat and its time of growth, with photographic illustrations of nearly all the common species. A guide to the study of mushrooms, with special reference to the edible and poisonous varieties, with a view of opening up to the student of nature a wide field of interesting and useful knowledge. 4to. pp. x+609. *pls. 60. figs. 504.* Columbus, O.: The Ohio Library Co. 1908. $4.75.

All these things show the apprentice hand; but, though they mar the book, they do not so detract from its value that it may not be commended to the public for whom it is intended. It will indeed be a welcome addition to public, school, and college libraries, where there is always a demand for well-illustrated books of this kind, and it will probably do good service in awakening an interest in mushrooms. It certainly treats wisely the matter of testing the edibility of mushrooms and no one who follows Mr. HARD's advice will come to harm. Thus it has a real field of usefulness. But it is not for the mycologist; and, unless "of its kind" is a saving clause, it is by no means what is claimed by the publishers in their circular—"By far the most complete work of its kind ever attempted in this country."—C. R. B.

Trees and woods

The fourth volume of the series on *Trees* by the late H. MARSHALL WARD has recently come from the Cambridge University Press.[2] With a fifth now in press the series will be concluded, for although the author had planned another, it was too inchoate to permit publication. The present volume has been issued under the editorial supervision of PERCY GROOM, who has left the manuscript practically unchanged, but has had the labor of selecting the illustrations, which are both numerous and appropriate.

As the three preceding volumes have treated respectively the buds and twigs, the leaves, and the inflorescences and flowers, this one presents the fruits. After a general discussion of the morphology of fruits (part I, 59 pp.), the second part (94 pp.) gives a key to trees and shrubs, based on characters derived from fruits, and accompanied by figures of most of the species. Like the other parts of the series, this one will doubtless be useful in Great Britain, though it cannot be particularly serviceable in this country. It embodies a good idea, however, which might be applied to the trees of this continent.

The eighth part of SCHNEIDER'S *Handbook of deciduous trees* (the third section of the second volume) has lately issued from the press.[3] Like its predecessors, frequently referred to in this journal, it presents, in the most compact form possible, descriptions of the species of angiospermous trees, native or planted out in central Europe, arranged in the sequence of a dichotomous key, and illustrated freely. It seems a most thorough and practical book, but somewhat disconcerting as to nomenclature. Who of our foresters will give us something as good, but perhaps a little less condensed?

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[2] WARD, H. M., Trees: a handbook of forest botany for the woodlands and the laboratory. Vol. IV, Fruits. Cambridge Biological Series. 12mo. pp. IV+161. *figs. 147.* Cambridge: University Press. 1908. New York: G. P. Putnam's Sons. $1.50.

[3] SCHNEIDER, C. K., Illustriertes Handbuch der Laubholzkunde. Charakteristik der in Mitteleuropa heimischen und im Freien angepflanzten angiospermen Gehölz-Arten und Formen mit Ausschluss der Bambuseen und Kakteen. Achte Lieferung (dritte Lieferung des zweiten Bandes). Imp. 8vo. pp. 241–366. *figs. 166–248.* Jena: Gustav Fischer. 1909. *M* 4.

The second part of JANSSONIUS' elaborate micrography of the woods of Java[4] has recently come from the press. In the notice of the first part of this work[5] we described the plan, which is here merely extended. The part includes in the concluding section of the first volume (Dicotyledones, Polypetalae, Thalamiflorae) descriptions of 67 species, in addition to the 108 of the first section. The second volume begins the Disciflorae and presents 54 species. The complete work will certainly be a monument of industry and will be serviceable for the microscopic identification of Javanese woods. That the game is worth the candle, we may be permitted to doubt.—C. R. B.

Microscopy of technical products

Now that so much attention is being paid to the purity of foods, drugs, and manufactured products of all kinds, it becomes of the greatest importance to have adequately trained men in municipal, state, and national offices, to whom can be submitted the many questions that are sure to arise as to the adulteration or sophistication of marketed articles. Unfortunately the number of competent persons is far short of the demand, and this state of affairs is sure to continue for some time. In this situation the only recourse is to have accurate handbooks in which may be found detailed descriptions of the characteristics, chemical and microscopic, of all the commoner substances which enter into commerce. Then one who has a reasonable familiarity with microscopic manipulation may be able to determine the more obvious cases of adulteration, and by experience may acquire real expertness.

To put into reach of American laboratories one of the most valuable of foreign works, Dr. A. L. WINTON, chief of the Chicago Food and Drug Laboratory of the Department of Agriculture, with the assistance of Dr. KATE G. BARBER, has translated an edition of HANAUSEK'S *Lehrbuch der technischen Mikroskopie*, which represents the last German edition extensively revised by the author.[6] The translators have also included a considerable amount of new material, and in particular they have incorporated into the key to economic woods—a most valuable feature of the book, permitting one to determine most of the species from a fragment of the wood—the American species of commercial importance. The illustrations have also been improved and augmented.

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[4] JANSSONIUS, H. H., Mikrographie des Holzes der auf Java vorkommenden Baumarten; im Auftrage des Kolonial-Ministeriums unter Leitung von Dr. J. W. MOLL bearbeitet im Anschluss an "Additamenta ad cognitionem florae arboreae javanicae auctoribus S. H. KOORDERS et TH. VALLETON." Zweite Lieferung. 8vo. Vol. I, pp. 369–568. Vol. II, pp. 1–160. *figs. 45–95*. Leiden: E. J. Brill. 1908. *M* 6.

[5] BOT. GAZETTE **43**:345. 1907.

[6] HANAUSEK, T. F., The microscopy of technical products. Revised by the author and translated by ANDREW L. WINTON, with the collaboration of KATE G. BARBER. Imp. 8vo. pp. xii+471. *figs. 276*. New York: John Wiley & Sons. 1907. $4.75.

The work opens with a section on the construction and use of the microscope, its accessories and reagents. The important types of technical products that are treated are the following: starches and inulin; vegetable fibers, including hairs, with a section on the examination of paper; animal fibers, mineral fibers, and textile fabrics; stems and roots, including woods (gymnospermous, dicotyledonous, and monocotyledonous), barks, and rhizomes, with some practical examples of the problems that are submitted for solution; leaves, under which only sumach leaves are treated; flowers, with insect powder alone treated; seeds and fruits, including a large range of oil cakes; and finally teeth, bone, horn, etc.

Of course in such a list there must be an end somewhere, for space is not unlimited; but one wonders at the basis of some choices. The line between drugs, foods, and technical products is not an easy one to draw; but if wheat and barley appear among the fruits, why not maize and rye? If sumach leaves, why not tea and tobacco? If insect powder, why not saffron? But it behooves us to be thankful for what there is, rather than to complain of what there is not. And what there is is sure to be thoroughly helpful.

The publishers' part has been well done. The illustrations are well printed, the text clear, and the binding substantial. The book is essential for public libraries and for governmental and university laboratories.—C. R. B.

Works of Léo Errera

We have already noticed in these pages the sumptuous republication of the work which, under the direction of LÉO ERRERA, issued from the botanical institute of the University of Brussels. In these volumes[7] his own original work takes a conspicuous place. But he did much other writing, popular, pedagogic, philosophic, literary, which is to be preserved by original publication or reprinting in a series of six volumes now being issued under the title *Recueil d'œuvres de Léo Errera.*[8] Of these three have appeared. Two deal with botanical subjects and one contains verse and prose on a variety of topics—addresses, thoughts, philosophic epigrams, etc. The botanical topics of the first volumes are: A letter on the vegetation about Nice; Agriculture and horticulture in Norway (largely a criticism of SCHÜBELER); Structure and modes of fecundation in flowers (200 pp.); Secondary heterostylic characters of primroses (a posthumous work completed by Miss J. WERY) (30 pp.); Progress of systematic botany; A neglected field of research (the efficacy of the defensive structures of plants); ENGELMANN'S bacterial method; Compass plants. In the second volume we find: Respiration of plants (one of a course of public lectures); De grâce, des noms latins (a plea for the avoidance of vernacular names); Scientific bases of agriculture (36 pp.);

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[7] Recueil de l'Institut Botanique Léo Errera. BOT. GAZETTE **43**:215, 347. 1907; **45**:201. 1908.

[8] Recueil d'œuvres de LÉO ERRERA. 8vo. Vols. I, II, Botanique Général. pp. iv+341. Vol. VI, Melanges (vers et prose). pp. xiv+222. Bruxelles: H. Lamertin. 1908.

Descriptive text of physiological charts (90 pp., including small reproductions of the charts which he published in conjunction with LAURENT); Letter prefatory to DE WILDEMAN'S *Flore des Algues de Belgique;* An elementary lesson on Darwinism (106 pp.; an admirably clear and brief presentation, which appeared first in 1900 and is now printed as he had revised it for a third edition). This volume closes with three posthumous articles: Plants in contrast with other beings; What there is in a plant; The *épopée* of a ray of sunlight.

These volumes, as well as the more strictly scientific ones, will form a worthy memorial of this distinguished *savant*, whose writing is always luminous and inspiring. His bibliography, though voluminous (287 titles, as we learn from an interesting biography just published[9]), is remarkable, not alone for its extent, but for its value. To have all his work collected is a real boon.—C. R. B.

NOTES FOR STUDENTS

Papers on mucors.—Two valuable papers, largely taxonomic in character, have recently appeared on the mucors. In two ways they show an advance over other taxonomic work in this confused group. In the first place the center for fungus cultures maintained by the *Association Internationale des Botanistes* has been made use of, and the species investigated were compared as far as possible with named cultures from this and from other sources. Provided contamination of cultures in the source of supply is avoided, this center in Amsterdam affords a ready method of checking up determinations and should be of increasing value to mycologists. In the second place the differentiation of species according to their sexual character into homothallic and heterothallic forms is recognized as an item in the classification, and in heterothallic species the production of zygospores, when a given strain is grown in contact with the opposite strain of a known species, is used to establish its specific identity with the form tested.

HAGEM[10] announces his paper as a preliminary contribution to a study of soil mucors. By exposing Petri-dish cultures to the air and allowing the spores which fall on them to develop mycelial colonies, he finds with SAITO that spores of the mucors, both absolutely and relative to other molds, are unexpectedly of infrequent occurrence in the air. Only seven species were thus found. In investigating the mucor flora of the soil, samples from different kinds of soils were sown on various nutrient substrata, and the resulting growths isolated in pure cultures. Sixteen different species, confined to the genera Mucor, Rhizopus, Absidia, and Zygorhynchus, were found, of which six are described as new, viz., *Mucor strictus*, *M. sphaerosporus*, *M. griseo-cyanus*, *M. silvaticus*, *M. norvegicus*, and *Absidia glauca*. Four new forms are added to the list of heterothallic species. One of these, *Mucor hiemalis*, was especially investigated as regards the distribution in nature of the two sexual races. From a total of 52 separate isolations, 21 were of one sex, 5 of the other sex, and 26 (50 per cent.) failed to give any reaction with the test strains and were listed as neutral. Three of the strains that took part in zygospore formation were very weak in their sexual activity, and one of them under further culture entirely lost its power to take part in zygospore formation. The distribution of the sexual races in this species is thus shown to be in accord with the condition in Rhizopus, where out of 59 strains investigated by the reviewer, 19 were (+), 27 (−), and 13 neutral. The large percentages of neutral races thus established for these two species, together with the reviewer's own experience with neutral races in other heterothallic species, renders it probable that sexual neutrality is a widespread phenomenon among the mucors. There is little at present known to indicate its cause or significance.

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[9] FREDERICQ, LEON, AND MASSART, JEAN, Notice sur LÉO ERRERA, membre de l'Academie. 12mo. pp. 153. Brussels: Hayez. 1908.

[10] HAGEM, OSCAR, Untersuchungen über norwegische Mucorineen, I. Vidensk.-Selsk. Skrifter. I. Math.-Nat. Kl. No. 7. pp. 50. 1908.

LENDNER,[11] in his studies of the Mucorineae of Switzerland, has not confined himself to mere local species, and though he has not attempted to present an exhaustive treatment of the whole group, he has given us a more or less critical arrangement of the genera Mucor, Rhizopus, and Absidia. In these three genera keys for the determination of species are given, and each form is described, either from the original description or from A. FISCHER, with additional notes on such species as he had himself cultivated. In classifying the genus Mucor, FISCHER'S division into the unbranched, racemosely branched, and cymosely branched groups is followed. Fifty-one species are recognized, of which seven, *M. lausannensis*, *M. genevensis*, *M. pirelloides*, *M. lamprosporus*, *M. Jansseni*, *M. spinescens*, *M. dimorphosporus*, are described as new species, and one, *M. adventitius* var. *aurantiaca*, as a new variety. BAINIER'S genera, Parasitella and Glomerula, are reduced to the genus Mucor, as also VUILLEMIN'S Zygorhynchus. The genus Mucor is the Crataegus among fungi and will probably always remain a taxonomic playground for mycologists. One might imagine that early systematists used the genus as a group to practice on, and their one- or two-line descriptions are frequently hardly sufficient to tell us whether the form described is a mucor or a myxomycete. Such supposedly common forms as *Mucor Mucedo* and *M. racemosus* among others, it is impossible to determine with any degree of accuracy, and therefore these designations can be considered hardly more than group names. We cannot but have considerable charity toward one who feels inclined, in consequence, to disregard the stock names, but when each mycologist who works on the genus gets out a list with names of his own, the result is confusing to a degree. Moreover, species shown to be distinct by the reaction between their sexual strains are frequently so closely related and vary so widely under different conditions of cultivation that the usual description is insufficient to distinguish them. LENDNER has done a service in bringing together the descriptions of species since FISCHER'S publication. We are grateful that he has not found it necessary to make new species out of more than 15 per cent. of the 51 forms listed. Seven circinellas are described, of which *C. minor* and *C. aspera* are given as new. In the genus Rhizopus, of which 22 species are recognized, physiological characters, such as ability or inability to grow on potato above 39° C. and power to ferment different carbohydrates, are used in addition to the usual distinguishing morphological characters. Material received from the Amsterdam center under the name of *Mucor norvegicus* is identified as *R. nodosus*. Seventeen species are recognized in the genus Absidia, of which *A. spinosa*, a homothallic and heterogamic species, is described as new. In addition to the forms from the genera mentioned, *Cunninghamella elegans* is described as new.

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[11] LENDNER, ALF., Les Mucorinées de la Suisse. Matériaux pour la flore cryptogamique Suisse. Vol. III, Fasc. I. pp. 180. 1908.

In addition to the systematic part of 113 pages, an introduction of 47 pages is devoted to methods of isolation and cultivation, and to a discussion of the sexual reproduction in the group, together with the results of a cytological investigation of the formation of zygospores. It might be expected that forms in which the sexual differentiation had extended to the separation of distinct male and female races would show a differentiation in the uniting gametes. In no heterothallic form, however, has there been shown to be any constant difference in the size of the gametes, such as occurs in a few of the homothallic species, where, since the zygospores are produced between neighboring filaments of the same plant, a less specialized sexual condition might be supposed to exist. In *Absidia Orchidis*, LENDNER finds that the circinate outgrowths, which typically arise from both suspensors, are at times produced from but one, which has been cut off from the large progamete that he considers female. This he claims an indication of sexual differentiation, as also the frequent inequality in the gametes of Rhizopus. From these facts he concludes that the (+) and (−) races are potentially homothallic, but with the opposite sex more or less completely suppressed. The suggestion that the sexual races may be potential hermaphrodites is in line with our knowledge of higher forms, but to formulate this as a conclusion and to claim that the smaller and larger gametes formed by a single sexual race are male and female respectively, as LENDNER would imply, is certainly going beyond the facts in hand. The reviewer has shown that in Rhizopus the larger gamete is derived sometimes from the (+) and sometimes from the (−) plant, and that similarly in the heterothallic species of Phycomyces the outgrowths (which LENDNER, p. 38, wrongly says arise from the zygospore itself) are confined sometimes to the (+) and sometimes to the (−) suspensor. The inconstant difference in size of gametes and behavior of outgrowths from the suspensors in *Absidia Orchidis* is probably merely nutritive in character and of no sexual significance. In *A. Orchidis* also, is figured what appears to be an arrested stage in the formation of a zygospore between two outgrowths from the same suspensor, and therefore belonging to the same sexual race. If this is used as an argument for the contention just mentioned, the fact should be established beyond doubt. Even if the author were not mistaken as to the terminations of the filaments apparently in conjugation, which would be difficult to follow in a tangle of other filaments, these two arrested gametes might be thought to have arisen adjacent to each other at the stimulus of contact of a third branch, which came from the opposite sex but had remained in only temporary contact with them.

No two investigators are as yet in accord as to the cytology of the zygospores of the mucors. GRUBER, who apparently has done the most careful work on the zygospores of Sporodinia, was unable to find a fusion of nuclei at any stage in their formation or maturation, and several of the most experienced of American and European cytologists of the fungi have personally told the reviewer that they also have investigated the zygospores of this same species, but with no better results. In 1906, DANGEARD, working with *Mucor fragilis*, described the uniting cells as gametangia and saw a fusion of nuclei in pairs soon after the union of the two sexual cells. The condition in Sporodinia was more difficult to follow, but DANGEARD believed he was able to find the same condition in the zygospores of this species. LENDNER, in the work before us, criticizes the conclusions of DANGEARD, claiming that the figures which DANGEARD interprets as stages in fusion are in fact stages in division, since they occur at the same time in the two suspensors as well. What DANGEARD considers as degenerating supernumerary nuclei toward the periphery of the zygospore, LENDNER never finds in degeneration, and he believes them to be in this position to preside over the formation of the membrane. The real sexual fusion, according to LENDNER, is between two large nuclei which approach the center of the zygospore. The two densely staining bodies in the fusing nuclei, which are homologized with chromosomes, give at first four bodies in the fusion nucleus, that eventually are reduced to two and finally unite into a single mass. Neither DANGEARD nor LENDNER has studied the germination of the zygospores.

Since KLEBS showed that external factors are responsible for the form of reproduction in Sporodinia and many other fungi, the influence of external conditions upon the growth and reproduction of individual species has become a favorite subject of investigation. As the reviewer has shown, external conditions are more influential in determining the form of fructification in the two homothallic species of Sporodinia and Dicranophora, found growing on fleshy fungi, than in the homothallic species, *Zygorhynchus Moelleri*, recently investigated by WISNIEWSKI,[12] a pupil of RACIBORSKI. It seems to be generally true in regard to the influence of external conditions, that the limits within which zygospore formation is possible are narrower than those within which sporangial formation occurs. WISNIEWSKI finds that, although under ordinary conditions sporangia are formed together with zygospores on the same mycelium, extreme conditions may suppress the production of zygospores, while sporangia are still formed. On pure agar below 5° C. and on the same substratum in direct sunlight, only sporangia will be produced. (It may well be the heat rather than the light effect of the direct rays of the sun that is here influential.) Under all other conditions examined, both zygospores and sporangia were produced together, if at all. The decrease in relative abundance of zygospores is associated with a checking of the rapidity of growth of the mycelium. The transpiration is shown to have no effect upon the rapidity of growth, and it is assumed that for this reason increase or decrease of moisture in the surrounding air does not affect the proportion between zygospores and sporangia. Upon certain substrata, zygospores are more abundant at the junction of adjacent mycelial colonies, forming dark lines. The conditions governing their production have not been investigated.

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[12] WISNIEWSKI, P., Einfluss der äusseren Bedingungen auf die Fruchtform bei *Zygorhynchus Moelleri*. Bull. Acad. Sci. Cracovie Cl. Sci. Math. et Nat. **1908**: 656–682.

For several years DAUPHIN has been interested in the genus Mortierella. In a recent paper on the genus[13] he gives in 28 pages a systematic arrangement of the species as an introduction to a special study of *M. polycephala*. The original descriptions and figures are given for each of the 29 species and varieties discussed. Two new species, *M. canina* and *M. raphani*, and one new variety, *M. van Tieghemi* var. *cannabis*, are described. The genus is divided into four group species (*grandes espèces*) with subspecies (*petites espèces*) and varieties under them. A well-arranged key would have added to the value of this part of the work. *M. polycephala* is the only one of the Mortierellas which has been investigated in regard to the influence of external conditions upon the production of zygospores. In this species, which forms the subject of the physiological part of the paper, DAUPHIN has succeeded in finding the zygospores, and since he obtains them from sowings of single spores, he classifies the species as homothallic. This being the case, it seems strange that they have not been found in this form by other investigators, since as yet no neutral strains have been found for homothallic species. The optimum temperature for germination of the spores is placed at 27° C., and the optimum for formation of sporangia and zygospores, between 15 and 20° C. Germination and growth are checked by darkness, but the fructifications are not altered. Light increases the rapidity of development, but if too intense causes the fructification to be confined to stylospores. The violet and ultra-violet rays of the spectrum seem necessary for the germination of the spores. X-rays and the influence of radium are inhibitive to germination and growth, the radium in addition causing the production of cysts in the hyphae. Moisture in the surrounding air is shown to be necessary for the germination and growth of the fungus. Perfect development will take place in an atmosphere completely free from oxygen. A decrease, however, of atmospheric pressure below 150^{mm} causes the mycelium to remain sterile. An increase of pressure above atmospheric checks the growth of the mycelium without preventing the normal fructifications. *M. polycephala*, like other mucors, develops poorly in liquid media. The monosaccharids, especially dextrose and levulose, were found most favorable of the carbohydrates for formation of zygospores and sporangia. The influence of different concentrations of the nutrient was little investigated, but stylospores and sporangia were produced without zygospores when the amount of dextrose was increased from 20 per cent. to 60 per cent. The purpose of this part of the paper seems to have been to find out the influence of a large number of more or less isolated external conditions upon the form of fructification, rather than to work out thoroughly the influence of a few closely related factors.

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[13] DAUPHIN, JEAN, Contribution à l'étude des Mortierellées. Ann. Sci. Nat. Bot. IX. **8**:1–112. 1908.

It is hardly necessary in a botanical publication to comment on a recent note in *Science*, entitled *Mucor cultures.*[14] The author states that "in the study of the Mucoraceae for several years, some interesting facts concerning the development or rather non-development of zygospores were observed." In a thousand cultures of *Rhizopus nigricans*, made from material collected by the author or sent him by friends, as well as in five hundred specimens found growing spontaneously in different places, and in about five hundred other unrecorded observations of the fungus (a total of two thousand observations), no zygospores were found. Inoculations were made on a number of different media, including HAMAKER's corn-bread-muffin combination, and the growth of the cultures was tested in closed jars in H, N, and CO_2. No zygospores were obtained, and the conclusion is reached that "the absence of oxygen is not a necessary condition for the growth of zygospores." It is a pity that one who has the time to make observations on 2000 cultures should not have taken the trouble to read the recent literature on the subject, to learn in what part of a culture zygospores are produced and under what conditions their formation is possible, and so be in a position to make a contribution of some value. Additional information in regard to the relative distribution in nature of the two sexual strains of this most common of molds might have been the fruit of so extended a series of observations.

Appended is a list of species, the thallic condition of which has been determined, arranged according to the type of their sexual reproduction. Following each species is given in parentheses the name of the author who has investigated the zygospores and determined the sexual condition of the species in question.

Homothallic

1. Sporodinia grandis (BLAKESLEE)
2. Spinellus fusiger (BLAKESLEE)
3, 4. Mucors I and II (BLAKESLEE)
5. Mortierella polycephala (DAUPHIN)

Heterogamic

6. Dicranophora (BLAKESLEE)
7. Zygorhynchus Moelleri (BLAKESLEE)
8. Zygorhynchus heterogamus (BLAKESLEE)
9. Abisdia spinosa (LENDNER)

Heterothallic

1. Mucor Mucedo (BLAKESLEE)
2. M. hiemalis (HAGEM)
3. M. silvaticus (HAGEM)
4–9. Mucors III–VIII (BLAKESLEE)[15]
10. Absidia Orchidis (HAGEM)
11. Absidia glauca (HAGEM)
12. Absidia caerulea (BLAKESLEE)
13. Absidia repens (BLAKESLEE)
14. Rhizopus nigricans (BLAKESLEE)
15. Phycomyces nitens (BLAKESLEE)
16. Circinella umbellata (BLAKESLEE)
17. Cunninghamella echinulata (BLAKESLEE)
18. Choanephora cucurbitarum (BLAKESLEE)
19. Helicostylum piriforme (BLAKESLEE)
20. Syncephalastrum (BLAKESLEE)
21. MUCOR N, n. gen. (BLAKESLEE)

—A. F. BLAKESLEE, *Storrs, Conn.*

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[14] SUMSTINE, DAVID R. Science N. S. **29**: 267. Feb. 12, 1909.

[15] Perhaps some of Mucors III–VIII are identical with species already in the list.

Mesozoic Equisetales.—One great desideratum in discussions as to the origin of existing plants is an increase in our knowledge of those of the Mesozoic. At the present time the Paleozoic flora is much better understood than that of the intervening period, which gave rise to the characteristic groups of our existing flora. A contribution by HALLE[16] throws a good deal of light on the organization of the equisetum-like forms of the earlier Mesozoic (Upper Triassic and Lower Jurassic). The author describes the vegetative stems and cones of several Equisetales. He establishes a new genus, *Neocalamites*, which has the general habit of the Calamites, including the leaf whorl made up of ununited leaves, with the herbaceous texture of the existing equisetums. It further resembles Calamites in the fact that only every second internodal strand (or fewer) gives off a leaf trace in the region of the node, and in the fact that the internodal bundles are frequently continuous at the nodes, in contrast to the alternating condition found in Equisetum. In Equisetites the leaves are in united sheaths as in the living genus, but in some of the species described by the author the same continuous bundles, and leaf traces fewer than the internodal strands, as are found in the Paleozoic Equisetales, are described. In the smaller branches, however, the leaf strands correspond to the number of internodal strands, thus foreshadowing the condition found in the living Equisetum. Perhaps the most interesting feature of this important addition to our knowledge is the description of the cones, cone-scales, and spores of Equisetites. The two former do not differ strikingly from those of the living genus, but the spores, interestingly enough, show the absence of elaters and the presence of triradiate sculpture described for the megaspores and microspores of the Calamites. The cones are isosporous. This article connects in a very satisfactory way the organization of the Paleozoic Equisetales with that of those still living, and illustrates the important bearing of paleontological facts on any stable scheme of evolution.—E. C. JEFFREY.

Membrane of diatoms.—MANGIN presents[17] an account of some extended observations on the diatoms, especially those of the plankton. His most important observations relate to the membrane. This he finds to be composed of a substance identical with pectic compounds, combined more or less intimately with silica; the siliceous skeleton thus formed is impregnated and invested with a gelatinous membrane which often hides, at least in plankton species, the characteristic ornaments. He controverts the ideas of SCHÜTT as to the growth of the membrane (through agency of an extracellular plasma), which he discusses at some length; and after describing improved methods of staining the membrane (by ruthenium red, and by an *old* solution of hematoxylin with ammonium- or ruthenium-alum, which may be aged artificially), he gives some detailed examples in the study of certain species.—C. R. B.

---

[16] HALLE, T. G., Zur Kenntniss des mesozoischen Equisetales Schwedens. Kung. Svensk. Vetenskapsakad. Handl. **43**: No. 1. 1908.

[17] MANGIN, L., Observations sur les Diatomées. Ann. Sci. Nat. Bot. IX. **8**:117-219. *figs. 14.* 1908.

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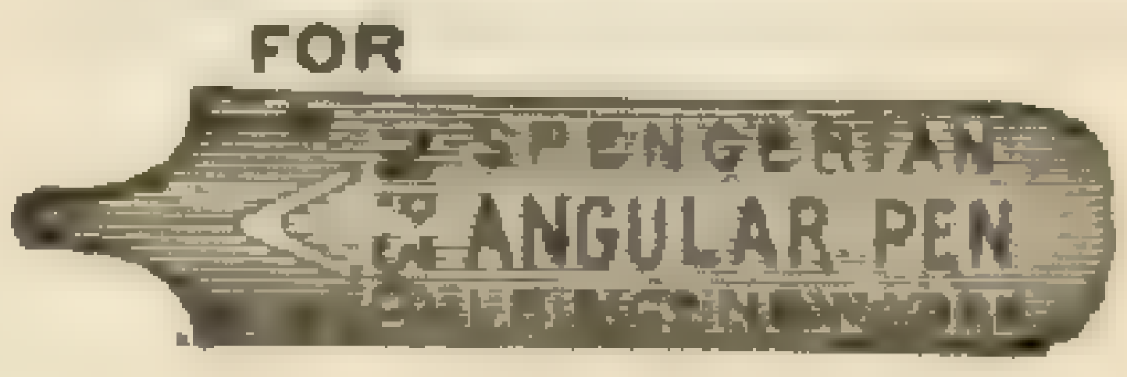

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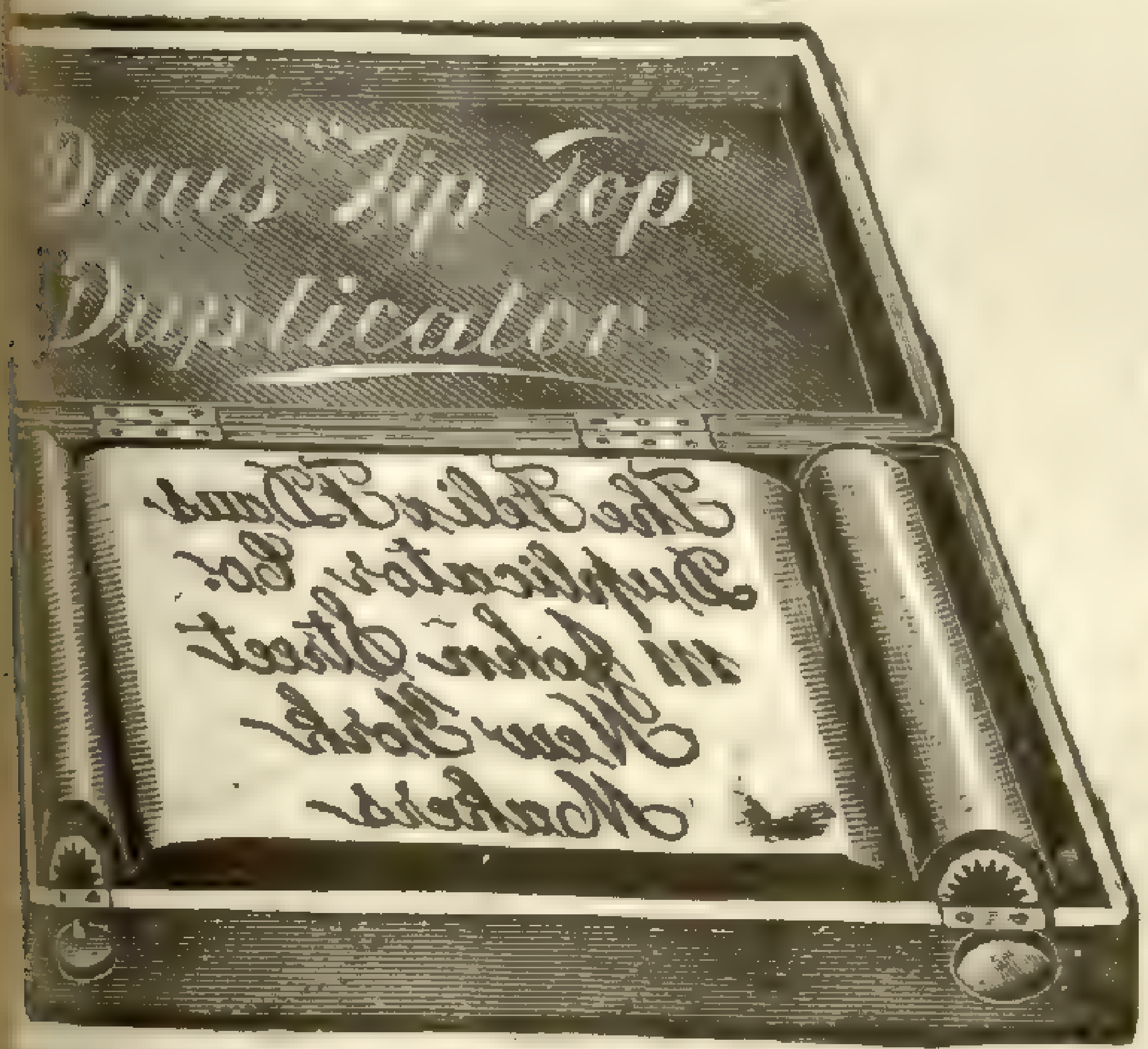

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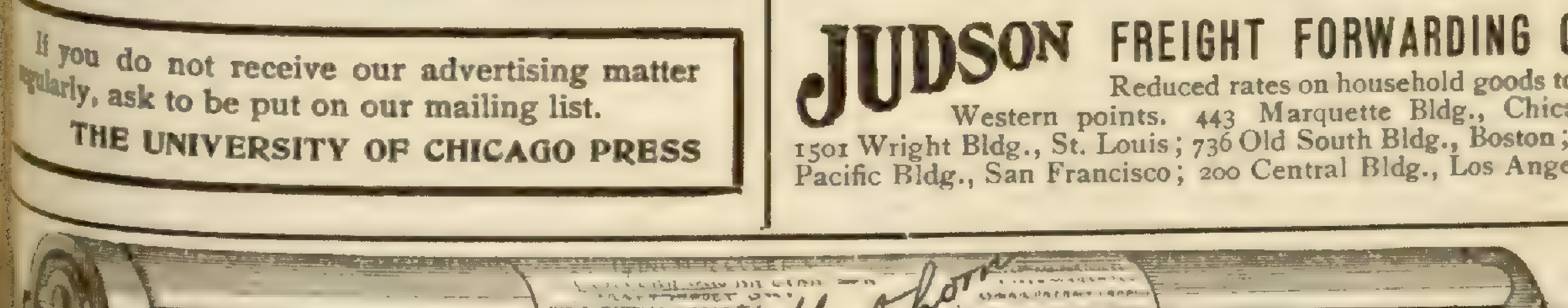

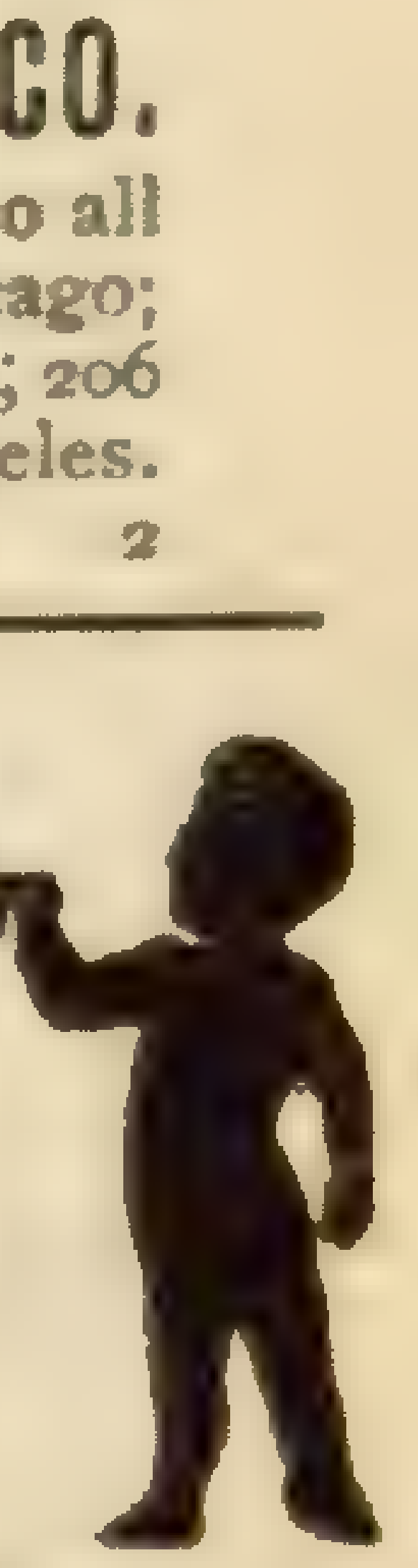

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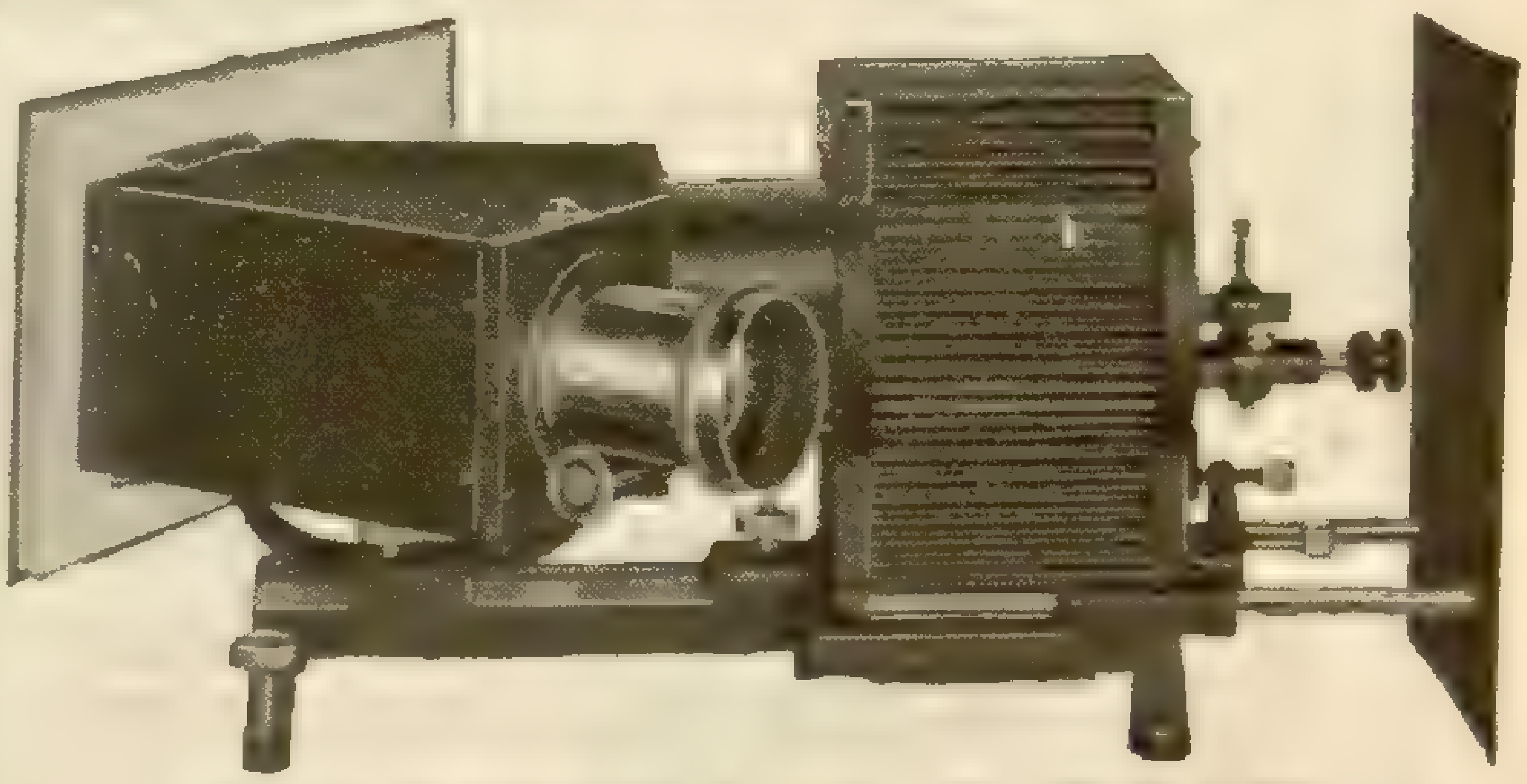

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June 1909

Editors: JOHN M. COULTER and CHARLES R. BARNES

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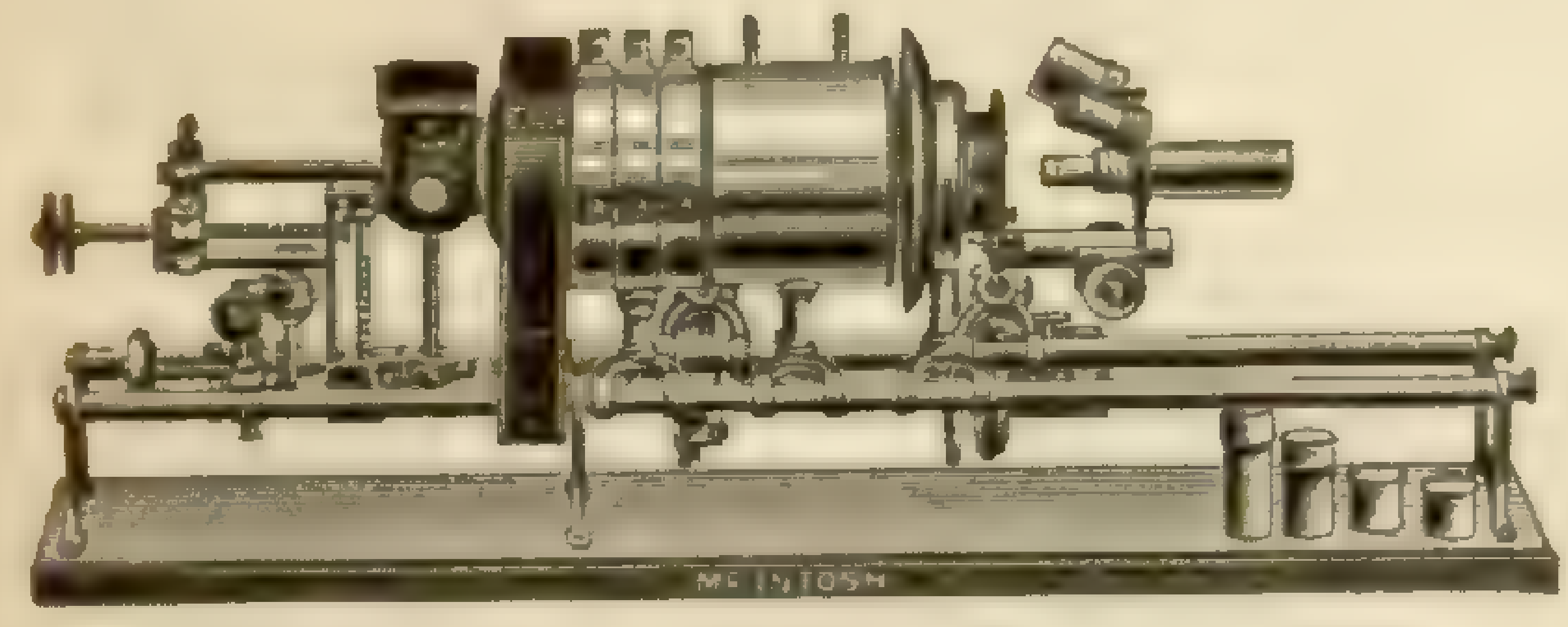

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VOLUME XLVII NUMBER 6

BOTANICAL GAZETTE

JUNE 1909

CONTRIBUTIONS FROM THE ROCKY MOUNTAIN HERBARIUM. VIII

AVEN NELSON

In 1905 Mr. LESLIE N. GOODDING again made some collections in the deserts of southern Nevada and adjacent Arizona. These plants, like those of his collections of 1902 and 1903, were deposited with the Rocky Mountain Herbarium at the University of Wyoming, to be named and distributed. Interesting as the earlier collections proved, these which came from even more inaccessible places and from regions which represent the extremes of aridity and heat are equally so. I submit herewith descriptions of the new species and notes upon others that are but little known or that seem to need generic differentiation.

PLANTAE GOODDINGIANAE

Calochortus comosus, n. sp.—Glabrous: bulb small, 8–12^{mm} in diameter, covered with dead sheathing flaky scales which also invest the base of stem: stem very slender, slightly flexuous, 1–2^{dm} high, 1 (rarely 2)-flowered: leaves narrowly linear: sepals lance-linear, as long as the petals: petals pale lavender or lilac, with darker lines, but not marked with spots or bands of other colors, broadly triangular-ovate, 18–25^{mm} long; the apex subtruncate, slightly undulate-dentate; the gland large, ovate, inordinately densely long-bearded with yellow hairs which are glandular-thickened toward the apex; similar hairs are scattered over all the lower half of the petal: anthers white, acute, 7–8^{mm} long; the filament as long: capsule acute-angled.

Las Vegas, Nevada, in limestone washes, May 8, 1905, *Goodding* 2323.

Probably most nearly allied to *C. flexuosus* Wats., from which it is readily distinguished.

Mirabilis limosa, n. n.—*M. glutinosa* A. Nels., Proc. Biol. Soc. Wash. **17**:92. 1904; not *M. glutinosa* Kuntze, Rev. Gen. **3**^{2}:265. 1898, the latter a Bolivian plant; *Hesperonia glutinosa* (A. Nels.) Standley, Contrib. U. S. Nat. Herb. **12**:365. 1909.

Lesquerella tenella, n. sp.—A delicately slender erect annual, 2–4^{dm} high, beginning to blossom when very small; uniformly but not densely stellate pubescent throughout: stems one or more from the summit of the slender tap root, unbranched: leaves rather distant, narrowly oblanceolate to linear, 1–4^{cm} long, usually tapering to a slender petiole: petals broadly spatulate, very obtuse or slightly retuse, about 8^{mm} long, twice as long as the lanceolate sepals: pod globose, not stipitate, about 5^{mm} long; the style about 3^{mm} long; the pedicel 10–15^{mm} long and variously curved and spreading or even reflexed.

Moapa, Nevada, April 8, 1905, *Goodding* 2184.

This species belongs in the section having immarginate seeds and with the annual species having globose pods; however, it has no known near relative.

Linum leptopoda, n. sp.—Having the appearance of a perennial but possibly only biennial, wholly glabrous, 3^{dm} or more high: root stout, with white furrowed bark, the caudex-like branched crown bearing several to many slender erect terete stems dividing into filiform branchlets above: leaves crowded below; those of the crowns scale-like, very short, 2–4^{mm} long and half as broad, leaving a crestlike scale when falling away; lower stem-leaves 5–12^{mm} long and 1–3^{mm} wide, becoming narrower, more distant, and finally bractlike above; stipular glands wanting: pedicels slender, 5–25^{mm} long: sepals about 5^{mm} long, green or brownish red, lanceolate, 1-nerved, with a few obscure glands on the margins as have also the bracts: petals a clear yellow, 7–9^{mm} long, broadly obovate or suborbicular, with obscurely crenate summit: stamens as long as the united part of the styles; the anthers large, as long as the filaments: styles united a little more than half their length: capsule about as long as the sepals, the false septum incomplete.

Las Vegas, Nevada, on stony slopes, May 4, 1905, *Goodding* 2276.

Except for the yellow flowers, this suggests at first glance *Linum Lewisii* rather than any of the yellow-flowered species.

Mortonia utahensis, n. sp.—*M. scabrella utahensis* Coville, ex. Wm. Trelease, Syn. Fl. N. A. **1**:400. 1897.

Specimens in full bloom, April 19, no. 2230, in the Muddy Range; fruiting specimens May 13, no. 2369, Las Vegas Mts., both localities in southern Nevada.

The excellent collections of this plant by Mr. GOODDING in 1905 leave no doubt that it ought to be considered distinct from *M. scabrella* Gray. Not only are the leaves uniformly much larger, but the flowers are very numerous and much smaller. The calyx-lobes equal and in fruit rather exceed the turbinate tube; they are broadly triangular, with erose scarious margins. The petals are nearly oval, with erose denticulate margins, and are narrowed abruptly to a short claw-like base; they barely equal the calyx-lobes and are never more than 3^{mm} long. The filaments are dilated downward. The leaves do not have revolute margins but are fleshy-thickened, looking as if bordered with cartilage.

Condalia divaricata, n. sp.—An intricately branched rigid shrub, $2–4^{m}$ high; the branchlets crowded, $3–7^{cm}$ long, strongly divaricate (at right angles to the stem), rigid, permanently covered with a fine close tomentum which at tip shades off to flaky deciduous scales, leaving the sharp brown spine free: leaves in approximate alternate fascicles, mostly on the spinelike branchlets, nearly sessile, somewhat thick and coriaceous, the margin wholly entire, permanently lanate-pubescent, oblong to oval, or sometimes narrowed toward the very short petiole, mostly obtuse at apex, the venation obscure, rarely more than the midrib showing, $4–8^{mm}$ long: flowers not known: mature fruit on very short peduncle and pedicels (each less than 2^{mm} long), the umbel apparently 3-flowered at most: drupe ellipsoidal, purplish black, $5–7^{mm}$ long (in dry specimens), the stone moderately thick-walled, completely 2-celled, with a large elliptical plano-convex seed in each cell.

Las Vegas, Nevada, in mature fruit, May 5, 1905, *Goodding* 2300.

The only species to which this is closely allied is *C. lycioides* Weberbauer, but that is a Texan species with narrower thin pale leaves conspicuously veined, and with subglobose fruit. The var. *canescens* of this species, at least as originally described (GRAY, Wheeler Rept. **6**:82), is a shrub only half as large, with greenish branches covered with a "gray powdery substance," leaves on petioles $4–8^{mm}$ long, and the spiny branchlets only $12–25^{mm}$ long. Though no specimens of the variety are at hand, it seems highly improbable that it is the same as the one now described. Should such prove to be true, it certainly deserves to be separated from *C. lycioides,* as is now done.

Mentzelia polita, n. sp.—Perennial, but probably short-lived:

root semi-woody, with a branched crown: stems 2 to several from the crowns, rather slender, erect, 2–4^{dm} high, somewhat cymosely branched at summit, glabrous, polished ivory white: leaves all entire; the lower narrowly spatulate-oblanceolate, sometimes abruptly acute, all but the lowest sessile; from the middle up linear, and the uppermost broadest at the base; all obscurely papillose, with a minute seta from the center of the papilla, and closely covered with microscopic pointlike hairs barbed at the summit: calyx-tube short-turbinate, about 5^{mm} long: petals white, spatulate, 10^{mm} long: stamens numerous, a few of the outer filaments dilated-petaloid but all fertile, shorter than the petals: style stout, not cleft at apex: capsule globose, crowned by the divaricate and now somewhat subulate calyx-lobes.

Las Vegas, Nevada, from washes in the hillsides, May 4, 1905, *Goodding* 2273.

Mentzelia synandra, n. sp.—Harsh and hispid throughout, duration not known (roots wanting in type collection): stems apparently several from the base, somewhat branched, 3–4^{dm} high, with long whitish aciculae and the short barbed pubescence of this genus: leaves mostly broadly elliptic-ovate, somewhat irregularly dentate, 3–6^{cm} or more long, the petioles usually much shorter; the upper surface bearing long aciculae with pustulate bases, and the lower long barbed hairs, both kinds mingling on the petioles and inflorescence: calyx-tube 10–14^{mm} long, somewhat exceeded by the linear-lanceolate lobes: petals 5, yellow, obovate-spatulate, abruptly acute, 3–4^{cm} long: stamens very numerous, all similar but the inner successively shorter; anthers oblong-oval; the filaments filamentous, not longer than the calyx-lobes, all connate at base, forming a firm thick-walled ring to which the petals cohere by their bases, the whole deciduous together from the firm rim of the calyx-tube: style stout, the 3–5 stigmas more or less convolute: fruit unknown.

Las Vegas Mountains, southern Nevada, May 13, 1905, *Goodding* 2373.

A very remarkable species, simulating the arrangement of petals and stamens in the Malvaceae.

Chylisma hirta, n. sp.—A coarse biennial, 3–5^{dm} high, branching from the lower part of the stem or from the crown, densely white-hirsute on the stems, less coarsely so on the leaves and sparsely on the pods: leaves mostly basal (the crown-leaves wanting in the type), very variable, 5–10^{cm} long or more, somewhat lyrate; the terminal lobe large, elliptic-ovate, irregularly crenate-dentate or entire; the lateral lobes irregular, small, few to many or even wanting: flowers large, crowded but ultimately evolving an elongated large-fruited raceme: calyx-tube turbinate, 4–5^{mm} long; its lanceolate lobes twice as long, with a short hornlike appendage near the tip: petals yellow, obovate-orbicular, about 15^{mm} long: stamens about equal; filament and anther each about 5^{mm} long: style shorter than the petals: capsules 5–6^{cm} long and 2–3^{mm} broad, on pedicels 5–15^{mm} long: seeds numerous, somewhat ovoid but irregular and angled through pressure, 2–3^{mm} long.

Tuly's Ranch, thirteen miles from Las Vegas, Nevada, in stony washes, May 1, 1905, *Goodding* 2348.

Lavauxia lobata, n. sp.—Biennial or possibly more enduring, the rather thick root with an enlarged more or less branched crown: stemless or more usually caulescent, softly and conspicuously hirsute throughout: leaves crowded on the crowns and short stems, 1–2^{dm} long, narrowly oblanceolate in outline, irregularly and deeply pinnately lobed; the lobes mostly oblong, obtuse or subacute, 5–18^{mm} long: calyx-tube 7–9^{cm} long; its lobes ovate-lanceolate and about 25^{mm} long: corolla yellow, changing to red with age; the petals as long as the calyx-lobes and a third broader than long: style as long as the petals, with long-linear stigmas: capsule linear-lanceolate, sharply angled but not winged, tapering very gradually from the base, 4–6^{cm} long, 4–6^{mm} broad: seeds 2–3^{mm} long, with conspicuous tubercle.

Meadow Valley Wash, Nevada, in sandy washes, April 7, 1905, *Goodding* 37 and 47 (type).

This fine species might readily be mistaken for a yellow-flowered Pachylophus, did it not have the angled capsule and tubercled seeds of Lavauxia.

Pachylophus cylindrocarpus, n. sp.—Biennial, stemless or more often developing a stoutish stem 1–2^{dm} high: leaves narrowly oblong-lanceolate, nearly entire to irregularly and lacerately dentate, almost glabrous on the faces but with a white fringe of soft hair on the margins; blade 5–15^{cm} long, on petioles as long or longer: calyx (including ovary) softly white-hirsute; its lobes linear-lanceolate, nearly 3^{cm} long: petals broadly cuneate-obcordate, with deep sinus, equaling or exceeding the calyx-lobes: capsule nearly glabrous, narrowly cylindrical-oblong, $4-6^{\mathrm{cm}}$ long, on a pedicel about 1^{cm} long; a double row of small sharp crests on each obtuse angle: seeds light brown, $2-3^{\mathrm{mm}}$ long, obscurely bidentate at apex, the raphal furrow conspicuous.

Carson's, Meadow Valley Wash, southern Nevada, May 26, 1902, *Goodding* 960a.

Quincula lepidota, n. sp.—Very pale as if canescent, but without pubescence except minute white pustular scales which are very numerous on calyx, pedicels, and petioles, and occur sparingly on the veins: perennial from rather thick rootstocks, the stoutish stems arising at intervals either singly or in clusters: stems erect, short (probably not much exceeding 1^{dm} in length even at maturity): leaf blades fleshy, mostly oval, from entire to undulate crenate, $12-25^{\mathrm{mm}}$ long, the narrowly margined petiole usually longer: pedicels slender, $10-25^{\mathrm{mm}}$ long: calyx-lobes triangular, shorter than the $2-3^{\mathrm{mm}}$ long tube: corolla $12-14^{\mathrm{mm}}$ long and broad, campanulate-funnelform, purple, with an orange-yellow band running from the middle of each lobe toward the base of the tube, where there is a crown of 5 woolly crests, the 5 slender filaments alternating with the crests: style longer than the filaments but shorter than the corolla; ovary glabrous: fruiting calyx and berry not known.

Dry Lake, Nevada, in the gumbo soil of a dry lake bed, April 17, 1905, *Goodding* 2232.

The appearance of this species is so different from that of *Q. lobata*, the only other species of the genus, that were it not for the character of the pubescence and the crown in the base of the corolla one would refer it, in the absence of fruit, to Chamaesaracha rather than to Quincula.

Physalis genucaulis, n. sp.—Perennial from a stout woody tap root, 1^{dm} or more long; densely but minutely pruinose or viscid puberulent throughout, and with no long hairs: stems several, each more or less branched; the branches with short zigzag internodes, $2-3^{\mathrm{dm}}$ high: leaves ovate to ovate-triangular, the base varying from abruptly cuneate to cordate, $1-3^{\mathrm{cm}}$ long: calyx campanulate, about 5^{mm} long, the triangular lobes about half as long as the tube: corolla greenish yellow, without conspicuous spots, campanulate-funnelform, about 10^{mm} long: style shorter than the corolla and just surpassing the oblong anthers: fruiting calyx equally but not conspicuously 10-angled, noticeably reticulate-veined, ovoid, with sunken base and connivent lobes closing the orifice.

Mesquite Well, southern Nevada, May 1, 1905, *Goodding* 2247.

One might think of referring this to *P. crassifolia* Benth. were it not for character of the fruiting calyx, or to *P. muriculata* Greene, if dealing with the vegetative characters alone.

— AMPHIACHYRIS FREMONTII **spinosa,** n. var.—Intricately and divaricately branched, many of the branches naked and slenderly spinose, floriferous twigs not surpassing the foliar ones; scabro-puberulent on foliage and young twigs: leaves oblong to elliptic, acute at both ends, 5–12^{mm} long: heads congested-glomerate: ray sharply 3-toothed.

Moapa, Nevada, April 8, 1905, *Goodding* 2199.

HYMENOCLEA FASCICULATA A. Nels., BOT. GAZETTE **37**:270. 1904.

MR. GOODDING again secured this species, this time at Cane Springs, Meadow Valley Wash, Nevada. These specimens are in perfect accord with the type collection, no. 662, Kernan, Nevada.

HYMENOCLEA FASCICULATA **patula,** n. var.—Slender stems (7–10^{dm} long) widely procumbent or drooping; branchlets assurgent from the stems upon which they are uniformly placed, and not fasciculately clustered at the ends; the very short floriferous twigs similarly distributed upon the branches, and the little glomerules of 3–5 heads (staminate and pistillate) open racemosely or almost spicately arranged upon the branches: involucral bracts of the staminate heads nearly entire; those of the pistillate heads very broadly reniform.

Moapa, Nevada, April 8, 1905, *Goodding* 2178.

BAILEYA PLENIRADIATA **perennis,** n. var.—Stems numerous, crowded in a dense cluster on the crown of a large indurated root, 3–5^{dm} high, leafy almost to the summit.

Moapa, Nevada, April 8, 1905, *Goodding* 2176.

Typical *B. pleniradiata* is an annual. This perennial form is more robust, and has a larger number of bracts (about 40) in the involucre and more disk-flowers (60–75). As pointed out by HALL (Comp. S. Calif. 164), the original *B. multiradiata* Harv. & Gray (Emory Report 144) is not the *B. multiradiata* Gray of Syn. Fl. **1**:318, but is the var. *nudicaulis* of that work.

Gaillardia pedunculata, n. sp.—Winter annual or biennial, 2–4^{dm} high: stems few to several from the crown of the slender tap root, leafy on the lower one-fourth only, the rest being the slender monocephalous peduncle, softly cinerous-hirsute: leaves irregularly pinnatified to entire, oblanceolate to linear, 2–6^{cm} long, more or less petioled, slightly viscidly pubescent especially when young: involucral bracts in about 2 rows, moderately whitened with flat woolly hairs, shorter than the disk which is 12–14^{mm} wide and high: rays 2^{cm} or less long, clear yellow, minutely pubescent on the outside, cleft one-third their length into lanceolate lobes, tapering cuneately from summit to the short very slender tube: disk-flowers also yellow; limb tubular, densely and minutely pubescent with beaded hairs: pappus of very thin paleae about as long as the inordinately pubescent achene, much shorter than the disk corollas, narrowly to broadly elliptic, mostly obtuse, and without costa or awn: fimbrillae of the receptacle nearly obsolete, consisting of a few short slender teeth.

Moapa, Nevada, April 8, 1905, *Goodding* 2177.

This seems to have no near relative among described species.

Enceliopsis, nov. gen.—*Enceliopsis* Gray, Proc. Am. Acad. **19**:9. 1883, and Syn. Fl. **1**: 283. 1894, as Section I of Helianthella.—Xerophytic plants, perennial from an indurated branching caudex, the crowns of which bear the rather thick simple leaves and the single long pedunculate monocephalous scape. Leaves canescent, and the petioles usually margined and longer than the blade. Heads large; the involucral bracts in 2 or 3 series. Bracts of the receptacle chaffy, hyaline, or scarious with greenish tip, and more or less conduplicate. Rays (rarely wanting) yellow, conspicuous, pubescent on the exterior, 20–40. Disk-flowers also yellow, with short narrow tube, abruptly expanded into the longer cylindrical throat. Achenes flat, oblong-cuneate, with narrow callous margins and the broadly retuse summit with a wider crownlike callus, from densely to thinly villous. Pappus of two subulate awns and in some species a narrow fringe of confluent squamellae between them; rarely even the awns wanting.—Plants peculiar to the "limestone clays" of the desert Southwest (southern Utah and Nevada, and adjacent Colorado, New Mexico, and Arizona).

The species for which this new genus is proposed were most of them described under Encelia, but have in more recent years been transferred to Helianthella, and sometimes back again. This of course indicates that they do not conform to either genus, and since the five species constitute a very homogenous and characteristic group it seems far better to give them generic rank. *E. nudicaulis*, though not the oldest of the species, was the first to be correctly and completely delineated, and may be cited, therefore, as the type of the genus. Mr. MARCUS E. JONES has well called attention to the fact that these are singularly out of place in Helianthella so far as habitat is concerned. The true species of that genus belong in the mountains, mostly in cold moist situations in high altitudes; while Enceliopsis occurs only in absolutely the hottest, driest area to be found on this continent.

Enceliopsis nudicaulis, n. comb.—*Encelia* (§ GERAEA) *nudicaulis* Gray, Proc. Am. Acad. **8**:656. 1873; *Helianthella nudicaulis* Gray, Proc. Am. Acad. **19**:9. 1883; *Encelia nudicaulis* Jones, Proc. Calif. Acad. Sci. II. **5**:701. 1895.

Enceliopsis argophylla, n. comb.—*Tithonia argophylla* Wats., Bot. King's Rep. **5**:423. 1871; *E. argophylla* and *H. argophylla* Gray, in turn, as above; not *H. argophylla* Coville, Contrib. U. S. Nat. Herb. **4**:132. 1893; *E. argophylla* Jones, *l. c.* 702.

Enceliopsis grandiflora, n. comb.—*H. argophylla* Coville, Contrib. U. S. Nat. Herb. **4**:132. 1893; *E. grandiflora* Jones, *l. c.* 702; *H. Covillei* A. Nels., BOT. GAZETTE **37**:273. 1904.

Enceliopsis nutans, n. comb.—*E. nutans* Eastwood, Zoe **2**:230. 1891; *Verbesina scaposa* Jones, Zoe **2**:248. 1901.

Enceliopsis tuta, n. sp.—The large woody root crowned with a widely and freely branching caudex; the branches thick, 2–10^{cm} long, protected from desiccation by a thick felted sheath of white wool: leaves all on the crowns, densely and minutely appressed-cinerous or silvery white, rather small, 15–25^{mm} long, narrowly to broadly elliptic-ovate, mostly cuneately subacute at both ends; the barely margined petiole usually much longer than the blade: scape rather slender, 15–30^{cm} long: involucre hemispherical, 20–25^{mm} broad, its pubescence similar to that of the leaves but longer; involucral bracts in about 2 series, narrowly lanceolate, the outer 9–11^{mm} long, the inner a little longer: rays puberulent, as in the other species, 20–25^{mm} long, linear, entire or 2–3-toothed at the slightly broadened apex: chaffy bracts of the receptacle equaling the disk-flowers: achenes softly hoary-villous, the dark body (when wet) in fine contrast to the white margin and crown, about 1^{cm} long, the slender incurved awns fully one-third as long and wholly free from and surpassing the hair on the achene: glandular waxlike particles occur abundantly on the flowers and free tip of the chaff.

Las Vegas, Nevada, May 4, 1905, *Goodding* 2271.

Chaenactis paleolifera, n. sp.—Biennial or possibly perennial: the tap root with an enlarged indurated crown bearing few to several freely branched stems, 1.5–3^{dm} high: leaves numerous, pinnately parted into few to several mostly short linear entire segments, canescently tomentulose as are also the stems and involucres: heads numerous, terminating the branchlets, naked pedunculate, 12–15^{mm} high and broad, 40–60-flowered: involucral bracts linear-lanceolate, slightly acuminate: receptacle convex, with numerous (as many as the flowers?) paleae; these linear, clavellate-acuminate above, and minutely glandular-pubescent, as are also the corollas, which exceed the paleae but little: corollas ochroleucous, essentially alike; their tubes a little shorter than the slightly enlarged throat: stamens included: stigmas exserted: pappus paleae 4, usually lance-acuminate and as long as the corolla-tube, sometimes shorter and obtuse, or slightly lacerate: achenes linear, slightly enlarged upward, and nearly terete, softly pubescent.

Tuly's ranch, 13 miles north of Las Vegas, Nevada, May 10, 1905, *Goodding* 2344.

Only two other species are accredited with paleae, *C. carpoclinia* and *C. attenuata* Gray, with 10 and 5 paleae respectively. These, apart from the differences in the number of paleae, cannot be confused with the species here proposed.

LEBETINA Cass. in Dict. Sc. Nat. **25**:394. 1822.—Among the several names to which the following species have been referred, Lebetina seems to be the earliest and the only one proposed especially for any of them. Dysodia, as at present constituted, includes most diverse things, and in the section EUDYSODIA extreme incongruity seems to have been reached (see GRAY, Proc. Am. Acad. **19**:37. 1883; HOFFMANN, ENGLER & PRANTL, Pflanzenfam. **4**^{5}:266. 1890). HOFFMANN assigns the first of the following to a section by itself, but had he added the other species the section would still have been fairly homogeneous and would have relieved the section EUDYSODIA. To think of *Dysodia papposa* and *D. Cooperi* Gray as congeneric stretches one's scientific imagination too far; therefore, I suggest the recognition of the genus Lebetina, with at least the species named below. These species in habit and habitat and in most essentials of structure are in close accord, the first being exceptional in having an extra series of paleae, and the first and second in that the style appendages are abruptly instead of gradually acuminate. The characters of the genus can be obtained from the description of the section EUDYSODIA and its subdivisions, as cited above, and in Syn. Fl. **1**:356. 1884.

Rather than leave these species in Dysodia, it were better to transfer them to *Porophyllum* Vaill, or to *Nicolletia* Gray, in either of which less violence would be done so far as appearance gives any clue to general conformity.

LEBETINA CANCELLATA Cass.—*Dysodia cancellata* Gray, *l. c.;* and Hoffmann, *l. c.*

Lebetina porophylla, n. comb.—*D. porophylla* Cav., Anal. Cienc. **4**:334; D.C. Prodr. **5**:639; not *D. porophylla* Willd., Enum. 900.

Lebetina speciosa, n. comb.—*D. speciosa* Gray, Proc. Am. Acad. **5**:163. 1861.

Lebetina porophylloides, n. comb.—*D. porophylloides* Gray, Mem. Am. Acad. **5**:322. 1855; and Bot. Cal. **1**:397. 1886.

Lebetina Cooperi, n. comb.—*D. Cooperi* Gray, Proc. Am. Acad. **9**:201. 1874; and Bot. Cal. **1**:397. 1885.

The collection of this last species by Mr. GOODDING (no. 2246, Mesquite Well, Nevada) led to a study of this group, which has convinced me that Dysodia will receive further segregation, though it may at the same time be expanded in certain other directions. HOFFMANN has thus referred *Thymophylla* Lag. (*Hymenatherum* Cass.), and has found it necessary to change the generic description in no essential character. For that reason the following may be referred to Dysodia.

Dysodia cupulata, n. sp.—Herbaceous perennial, from slender woody roots; puberulent on stems and leaves; foliage and involucre more or less beset with small round oil-glands; branching below: stems slender, less than 1^{dm} high, very leafy; branchlets terminating in a filiform naked monocephalous peduncle 2–4^{cm} long: leaves opposite below, pinnately parted into 3–5 filiform acerose lobes 1–2^{cm} long: involucres broadly campanulate or cup-shaped, about 5^{mm} high and broad; bracts about 16, completely united, 1 or 2 minute free bracts at base: rays about 12; ligule elliptic-oblong,

$2-3^{mm}$ long, fertile, yellow: disk-flowers also yellow, numerous, slightly exceeding the pappus, one sinus more deeply cleft than the others: pappus of 10 narrow paleae, united at base and in a single series, obscurely bidentate at apex, the mid-nerve continued from between the teeth as a minutely scabrous seta as long as the palea, the alternate paleae and setae shorter: achene linear subterete, obscurely ciliate-pubescent, $2-3^{mm}$ long, as long as the longer setae: stigmas obtuse.

Tuly's Ranch, Las Vegas, Nevada, May 10, 1905, *Goodding* 2343.

This is probably very near to *Hymenatherum Thurberi* Gray (Proc. Am. Acad. **19**:41 and Syn. Fl. **1**:358) and it may have to become *Dysodia Thurberi*. The description of that species is such as to make it difficult to settle the question positively in the absence of the type or of authentic material, but the geographical distribution makes their identity quite improbable.

Dysodia fusca, n. sp.—Pubescence minute, scurfy-glandular: plants low, $1-2^{dm}$ high, freely branched from a woody base; the ultimate branchlets very slender, fragile, white: leaves numerous, opposite, crowded (the internodes short), very narrowly linear, all or nearly all entire, mucronate, with few to several dark oval oil-glands: heads nearly sessile, campanulate-turbinate, $5-8^{mm}$ high: involucre cupulate, only the very short obtuse tips of the bracts free, with a few subulate accessory bracts at the base and with few to several oil glands: ligules oblong, 5–8, about 4^{mm} long: disk-flowers about as many, very narrow: anthers and stigmas included, the latter truncate, with an obscure apiculation: pappus paleae of both kinds of flowers wholly resolved into unequal scabrous capillary bristles as long as the disk corollas, fuscous and protruding brushlike from the involucre of mature heads: achenes linear, very finely striate, minutely pubescent, subterete, as long as the pappus: receptacle alveolate, naked, or with a few soft scattering hairs.

Muddy Range, southern Nevada, in a stony wash (three plants), April 10, 1905, *Goodding* 2214.

This seems to fall into GRAY'S section BOEBERA (Syn. Fl. **1**:356) and possibly may be allied to the two Mexican perennials mentioned. Those, however, have pedunculate heads and the leaves pinnately divided as is usual in the genus. Only the most liberal interpretation of the genus admits this species, and were it not for the gamophyllous involucre it were better to place it in Pectis, which it resembles in habit and in the opposite somewhat connate leaves.

PLANTAE MISCELLANEAE

Euphorbia manca, n. sp.—Annual, the decumbent base giving rise to few to several simple, erect branches 1–2$^{\text{dm}}$ high: leaves obovate-cuneate, broadly obtuse, numerous, the lower reduced: primary floral bracts ovate-reniform; the secondary broadly reniform, sometimes connate: inflorescence once or twice trichotomous: capsule about 4$^{\text{mm}}$ long: seeds short cylindrical-oblong, gray but not ashy, nearly smooth.

Mancos, Colorado, June 23, 1898, *Baker, Earle, and Tracy* 23.

This has been referred to *E. crenulata* Engelm. by NORTON in Rep. Mo. Bot. Gard. **10**:36. 1899. That species, as there constituted, however, is clearly an aggregate, both annuals and perennials being included even when of very diverse habits. The segregates readily discriminated seem to be as follows:

Perennial with branched stems from horizontal or ascending rootstocks; leaves crenulate; seeds with deep dark-colored pits. 1. *E. Nortoniana*
Annuals:
  Stems branched above; leaves crenulate; seeds ash-colored with irregular vermiculate ridges and broad shallow pits. 2. *E. crenulata*
  Stem branched from the decumbent base; leaves entire; seeds greenish gray, nearly smooth. 3. *E. manca*

E. crenulata is characterized adequately in the original description in Bot. Mex. Bound. 192; as well as in Wats. Fl. Cal. **2**:75 (as *E. leptocera*, an undoubted synonym); and in Greene, Man. Bay Region 80.

Euphorbia Nortoniana, n. sp.—*E. crenulata* of Norton in Rept. Mo. Bot. Gard. **10**:36. 1899, as to the perennial plant, from which the description is chiefly drawn.

Apparently common in California, the type selected being *Heller* 6625 (San Francisco, April 25, 1903) and 6486 (Pacific Grove, March 30, 1903).

In his key to the species of Euphorbia, NORTON provides for both the annual and the perennial plants (*l. c.* 8); and a very different plant from the above served for the figure on his *pl. 36*.

Gaurella canescens (Torr. and Frem.), n. comb.—*Oenothera canescens* Torr. and Frem., Fremont's Rep. 315. 1845; *Gaurella guttulata* (Geyer) Small, Bull. Torr. Bot. Club **23**:183. 1896.

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THE LEAVES OF PODOPHYLLUM

J. ARTHUR HARRIS

An inspection of the leaves of the flowering stem of *Podophyllum peltatum* shows that they are not exactly the same size. Furthermore, the larger one seems generally to be inserted a little lower on the axis than the other of the pair. HOLM (3) found that the two leaves do not develop simultaneously but that one appears before the other. Concerning this point he writes:

> Of its two leaves, the one is developed earlier than the other. The base of the petiole of this leaf is dilated into a pair of broad wing-like stipules which envelop each other and enclose a small green leaf and a flower bud; thus the two green leaves did not develop at the same time, as it might seem when we examine the plant during its flowering period with its leaves apparently opposite.

Some of the teratological literature has an interesting bearing upon this question of the differentiation of the leaves. PORTER (8) illustrates one type in which the flowering stem bears two leaves, the peduncle apparently originating from one of the petioles two or more inches above their insertion. In another form there are three peltate leaves with the peduncle originating between the upper two, which are represented as about equal in size and opposite,[1] or some distance above the fork from one of the petioles. One of the leaves may be much reduced in size, or but one leaf—then apparently terminal and with the peduncle lateral—may appear. Finally both leaves may be absent. FOERSTE (2), apparently unacquainted with PORTER'S paper, redescribes these forms and adds other types, similar in a general way. The production of a small, not peltate lamina upon the peduncle is not very rare. The instance observed by BAILEY (1) of a flower replaced by a small erect leaf, and mentioned by PENZIG (7) as *sehr wunderlich*, was probably merely due to the early abortion of the flower bud in such a case.

The essential point to be gained from the foregoing observations is that the flowering stem of Podophyllum, instead of producing only two opposite leaves, may become an elongated shoot of at least three leaves. In fact Britton and Brown in the *Illustrated flora* describe the species as "bearing 1–3 similar leaves or sometimes leaflets." The third leaf is frequently small and not peltate, but it may be very similar to the others.

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[1] Here probably belongs the case described by TRIMBLE (9) which PENZIG (7) records as not clearly expressed.

Knowing that more than two leaves are occasionally produced by the flowering stem, and that there appears to be a slight difference in the size and position of the two leaves in normal specimens, two questions occurred to me: (*a*) To what extent are the two leaves of Podophyllum really differentiated in type and variability? (*b*) What is the degree of similarity of leaves from the same individual?

A satisfactory measure of the area of a leaf so irregular as that of Podophyllum is obviously out of the question. It was necessary therefore to select some character other than size. The degree of lobing seems to be the only practicable one, although this character is not so definite as might be desired, and the determination is subject to considerable error due to personal judgment.

The margins of the very excentrically peltate leaves are irregularly toothed, lobed, or divided. It is quite impossible to draw a sharp line of distinction between the smaller lobes and the major divisions of the leaf, but I think that personal judgment would rarely vary greatly in the grading of an individual collection of plants. Perhaps less confidence is to be placed in a comparison of two or more lots taken at different times. In sorting the leaves into classes I counted as lobes the divisions extending at least half-way from the periphery of the leaf to the point of insertion on the petiole; divisions less sharply marked than this were not counted. Only normal plants—that is, those having only two leaves—were included in the collections. In sorting material to determine whether there is a differentiation between the upper and lower leaves of a pair, it is important that the appearance of the leaf lamina does not influence the judgment in any way. In dividing the nearly opposite leaves into upper and lower, the insertion of the petiole alone was examined. After the relative position of the two leaves was thus decided the counts were made.

The first lot of material examined was taken at Valley Park, near St. Louis, Mo., in May, 1906, when the plants were with partly grown fruit. In very few cases was there any question concerning the position to be assigned to the two leaves. All of the countings were made by myself on one afternoon, so that I think there can be but little error due to variation of judgment. All plants were taken at random, and none were discarded except because of mutilation which rendered the countings untrustworthy, save three which had an extra lamina at the base of the peduncle. The data for the 400 flowering stalks counted appears in the form of a correlation table as table I.

TABLE I

UPPER LEAF

		4	5	6	7	8	Totals
LOWER LEAF	5	1	4	3	..	..	8
	6	4	34	66	1	..	105
	7	1	52	144	28	..	225
	8	..	2	22	16	..	40
	9	..	..	6	10	1	17
	10	..	1	1	2	1	5
Totals...		6	93	242	57	2	400

The second series I secured in the woods at Palos, Athens Co., Ohio, in early July, 1908. It was really too late in the season to work to advantage, for many of the plants were so badly dried that they had to be discarded. I see no reason for believing that this discarding of individuals too brittle to be counted introduces any element of error into the work, though it did considerably increase the labor. The countings were made in as nearly the same manner as for the first series as possible. The data are given in table II.

TABLE II

UPPER LEAF

		2	3	4	5	6	7	8	Totals
LOWER LEAF	4	1	..	1	..	..	..	..	2
	5	..	..	13	24	..	..	..	37
	6	..	2	12	80	4	1	1	100
	7	1	..	9	121	42	8	..	181
	8	..	..	..	2	8	8	..	18
	9	..	..	..	..	1	..	..	1
Totals..		2	2	35	227	55	17	1	339

The physical constants for these two lots are laid side by side in table III. To permit of easy comparison the differences between the constants for the two series, and the probable errors of the differences, are given. Comparing the means for both upper and lower leaves for the two habitats, we notice that they differ by ten to twenty times the probable errors of their differences. The standard deviations differ by only one and a half to three times the probable errors of their differences. Perhaps the differences between the means of the collections from the two habitats are significant statistically, but I attach no biological importance to the differences, since they may be due merely to some slight local environmental condition. The variabilities certainly do not differ significantly.

TABLE III

VARIATION CONSTANTS FOR LOBING OF PODOPHYLLUM LEAVES

Series of material	Average and probable error	Standard deviation and probable error	Coefficient of variation
VALLEY PARK, MO.:			
Lower leaf	6.920± .029	.848± .022	12.25
Upper leaf	5.890± .022	.666± .016	11.30
Difference	+1.030± .036	+.182± .027	+ 0.95
PALOS, OHIO:			
Lower leaf	6.528± .029	.792± .021	12.13
Upper leaf	5.139± .027	.742± .029	14.43
Difference	+1.389± .040	+.050± .036	− 2.31
DIFFERENCES:			
Lower leaf	+0.392± .041	+.056± .030	+ 0.12
Upper leaf	+0.751± .035	−.076+.025	− 3.13

Taking now the question (*a*), that of a differentiation between the upper and lower leaves, we note that the means differ in both cases by about thirty times the probable error of their differences, and that the lower leaf has in both cases about one lobe more than the upper. The standard deviations differ by an amount which can hardly be regarded as significant. The relative variability as measured by the coefficient of variation is in one case higher for the upper leaf and in one case lower. After calculating the constants for the first series of material, I thought that perhaps the variability of the more distally placed leaf would be regularly lower than that of the more proximal one, as PEARL (4) found the variability of the whorls in Ceratophyllum to be. But the second series does not support this idea.

It may be interesting to compare the variability in the lobing of the leaves of Podophyllum with that of other leaf characters given by PEARSON (5). From page 361 I note the following values of the coefficient of variation for leaf characters:

Holly, Dorsetshire, prickles on leaves	26.29
Holly, Somersetshire, prickles on leaves	18.74
Ash, Dorsetshire, leaflets on leaves	18.65
Ash, Monmouthshire, leaflets on leaves	18.57
Ceterach, Somersetshire, lobes on fronds	18.25
Wild ivy, mixed, leaf-indices	17.77
Spanish chestnut, mixed, veins in leaves	15.72
Ash, Buckinghamshire, leaflets on leaves	15.46
Spanish chestnut, Buckinghamshire, veins in leaves	14.31
Beech, Buckinghamshire, veins in leaves	10.77

It appears by these comparisons that the lobing of the leaves of Podophyllum is rather less variable than leaf characters in general.

Turning now to the question of the degree of similarity between the two leaves, and calculating the coefficient of correlation between the number of lobes on the lower leaf and the number of lobes on the upper leaf by the familiar product-moment method, we find the correlations,

For the Valley Park series	.428 ± .028
For the Palos series	.468 ± .029
Difference	.040 ± .040

I was considerably surprised when these values turned up on my dividing machine. A priori, I would have expected considerably higher coefficients, say about .700, for the correlation between organs so closely associated as the leaves of Podophyllum. In thinking of the correlation between the leaves of Podophyllum, it had always seemed to me organic rather than homotypic in nature. The two leaves seemed so nearly exactly opposite and the whole "normality" of the plant seemed to depend so much upon their forming a symmetrical pair that I had expected the usual homotypic resemblance plus something more.[2] But instead we find values which fall directly in line with those found by PEARSON and others for homotypes in general. Taking merely the leaf characters noted above, we find the homotypic relationship calculated by PEARSON and his coworkers (**5**) to be the following:

Ceterach, Somersetshire, lobes on fronds	.631
Holly, Dorsetshire, prickles on leaves	.599

[2] For a clear statement of the distinction between organic and homotypic correlation see page 340 of PEARSON's splendid reply (**6**) to BATESON's criticism of the theory of homotyposis.

Spanish chestnut, mixed, veins in leaves	.591
Beech, Buckinghamshire, veins in leaves	.570
Spanish chestnut, Buckinghamshire, veins in leaves	.466
Ash, Monmouthshire, leaflets on leaves	.405
Ash, Dorsetshire, leaflets on leaves	.396
Ash, Buckinghamshire, leaflets on leaves	.374
Holly, Somersetshire, prickles on leaves	.355
Wild ivy, mixed, leaf-indices	.273

Some of these are slightly higher and some slightly lower than our coefficients; but when the probable errors attached to all constants are borne in mind, I think we cannot assert that our values are very different from those obtained by English biometricians for other leaf characters. Furthermore PEARSON shows reasons for considering some of his values too high and some too low for true homotypic relationships. For instance, ceterach is said by botanists to be largely influenced by growth and environment.[3]

There still remains one possible reason for thinking that the real correlation between the number of lobes on the leaves of the same flowering stalk may be somewhat higher than is indicated by these constants. The May apple spreads considerably by rootstocks. My plants from both habitats were taken from quite a wide stretch of woods, but a considerable number of the plants are doubtless vegetatively related. I do not believe this has a very large influence in my series, but it is proper to mention the point.

[3] From the arithmetical side there are also difficulties. I did not apply SHEPPARD'S correction for the second moment in calculating my standard deviations. Perhaps this should have been done, but until some mathematician works out the theory, biologists will not know what rule to follow in the case of integral variates. In the case of a range of variability so narrow as we have here, SHEPPARD'S correction would make a considerable difference, raising the coefficient of correlation by lowering the standard deviations. So perhaps our values should be a little higher.

There is also the question of leaves which fall on the borderline between n and $n+1$ lobes. In the present study I carefully tried to throw these into the class to which they most nearly belonged, just as one would have to do in the case of real integral variates. But after all, the lobing of the leaf of Podophyllum is not a case of discrete variation, and if I were repeating the work I would divide questionable cases between adjoining grades. Probably this would not make a very great difference in the end result.

The reader will note, too, that I am discussing "homotypic" correlation on series of material which I have just demonstrated to be differentiated. But I think I am quite justified in treating the material as I have done, for lower and upper leaves have always been kept separate. There has been no mixing of heterogeneous material.

Summarizing, we may say that so far as our materials show: (*a*) there is a sensible differentiation between the two leaves of the flowering stalk of Podophyllum in the number of lobes, but apparently not in the variability of the lobes, at least not in their relative variability; and (*b*) the correlation between the number of lobes on the two leaves of the stalk lies somewhere in the neighborhood of .45, agreeing well with the homotypic correlations for leaf characters in other species.

CARNEGIE INSTITUTION OF WASHINGTON

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A BOTANICAL SURVEY OF THE HURON RIVER VALLEY[1]

VII. POSITION OF THE GREATEST PEAT DEPOSIT IN LOCAL BOGS

GEORGE PLUMER BURNS

(WITH FIVE FIGURES)

The general appearance of the vegetation of the peat bogs in the Huron River valley has been fully described by TRANSEAU (**8**) and it is not necessary to give a detailed account in this paper. The plants are usually growing in a more or less regular zonal arrangement somewhat as follows: (1) open water with submerged plants, (2) water lilies, (3) floating sedge, (4) bog shrubs, (5) tamaracks, (6) maple-poplar, (7) willow or marginal zone.

There is wide variation in the position of the greatest amount of peat deposit and the width of the various zones. Even a casual survey of a number of local bogs emphasizes the fact that the open water is seldom in the center of the original post-glacial lake. The zonal arrangement is usually broken on one side, some zones being entirely lacking. In fact it is not uncommon to have all peat deposit lacking at certain places along the shore. According to some writers (**7**) the greatest accumulation of peat is found on the western side, in regions with prevailing westerly winds. In large basins which are only partly filled it is common to find open water occurring toward the eastern side. The wave-action produced by the westerly wind is supposed to hinder bog plants from obtaining a foothold on the eastern shore. The shoreward push of the ice is also a factor of importance in this connection (**8**, p. 418).

A study of the bogs near Ann Arbor soon revealed the fact that the greatest accumulation of peat on the western side was by no means common to all bogs. In fact the greatest variation was found within very short distances. At Dead Lake it is on the southern side (**1**); at Mud Lake, about one-half mile (800^{m}) west, it is on the northern side (**6**); at First Sister Lake, it is on the western side (**9**); at a small bog near Carpenter's Corner it is toward the east (**7**).

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[1] Contribution 112 from the Botanical Laboratory of the University of Michigan.

It seems, therefore, that some other factor must be sought. Plane-table maps were made of a number of bogs and the distribution of plants was carefully plotted. Contour maps of the bottoms of the original post-glacial lakes were then made. In making these maps a drill was made of gas pipe, cut in four-foot (1.2^{m}) lengths. To the end section was welded a carpenter's auger. With this drill, soundings were made through the peat to the clay bottom of the original post-glacial lake. A base line was run taking the longest diameter of the bog. Along this and at right angles to it, cross lines were drawn every hundred feet (30.48^{m}) in large lakes and every fifty feet (15.24^{m}) in small lakes. Borings were made at the intersections of these lines and every hundred or fifty feet on the cross lines. Near the shores it was necessary to make the borings closer, often every five feet (1.5^{m}). In bogs with open water it was necessary to make all borings through the ice, because it was impossible to hold a boat steady enough to bore through the peat without breaking the drill.

FIRST SISTER LAKE.[2]—This bog is situated a short distance west of Ann Arbor and has already been described by other writers (**8, 9**). It is surrounded on all sides by hills, except for three breaks. To the north was a small post-glacial lake; on the southwest corner it connected, by a narrow channel, with Second Sister Lake. The whole formed a very irregular chain of lakes draining into the Huron River.

The contour map of the bottom of the original post-glacial lake is shown by red lines in *fig. 1*. The heavy line indicates the margin of the original lake as indicated by the peat deposit. The shores rise somewhat abruptly on all sides. The lake had one basin. The deepest part was east of the center, the deepest point being fifty-four feet (16.5^{m}). From this point the bottom sloped gradually to the eastern shore. On the opposite side the forty-foot (12.17^{m}) contour made a wide divergence to the west; from this contour the bottom sloped gradually to the shore.

No attempt is made to show the flora of this early time. The black of *fig. 1* shows the arrangement of things as they were last summer. The open water occupies a very small area compared to what it did

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[2] Borings were made for the most part by Mr. HAROLD STEELE.

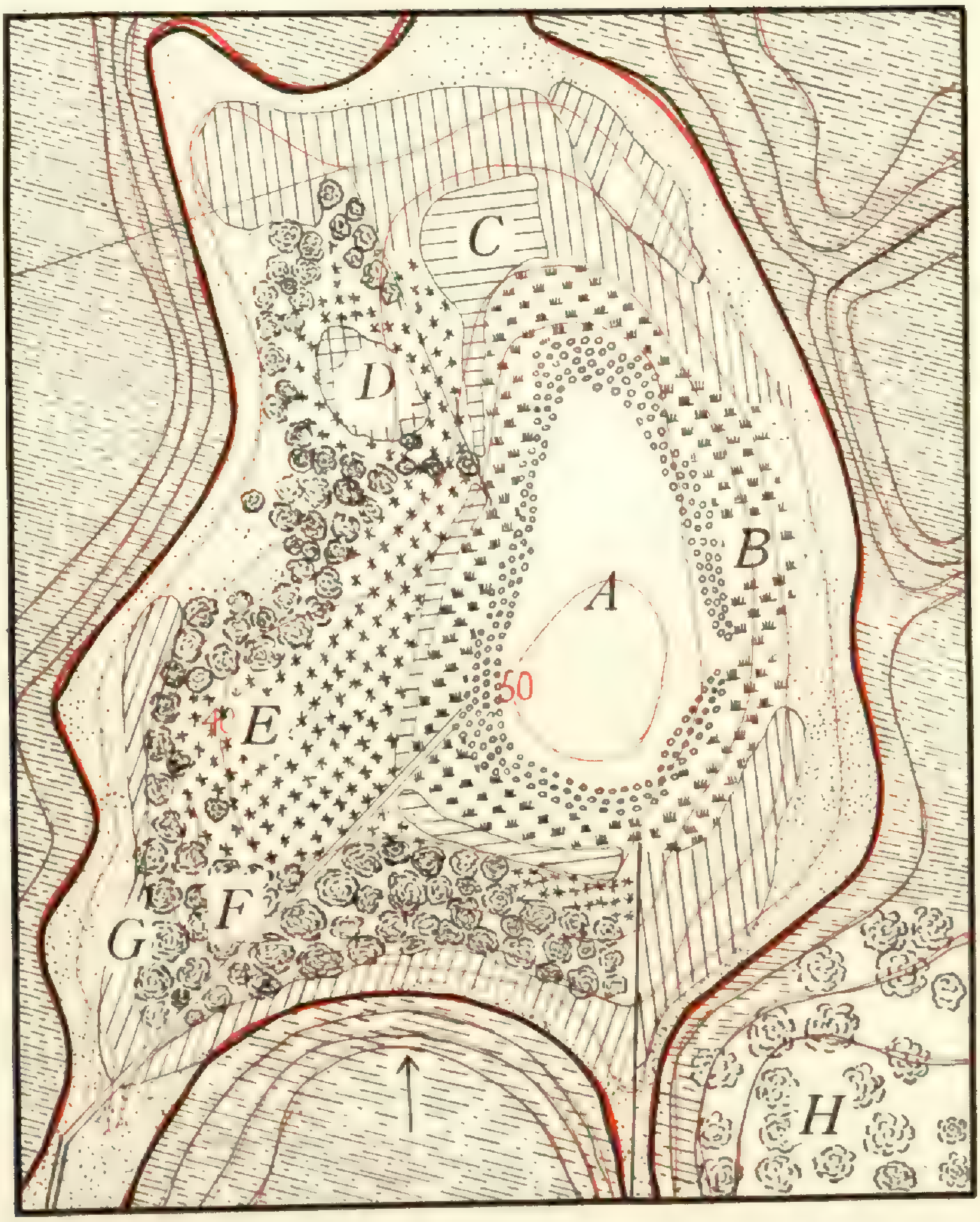

FIG. 1.—First Sister Lake. Contours of the post-glacial lake in red. The heavy line indicates the position of its shore as shown by peat deposit. Scale 1:2880. Contour interval of topography five feet, of hydrography ten feet.

Present distribution of plant societies in black. *A* open water; *B* bog sedge; *C* bog shrub; *D* clearing; *E* tamarack; *F* maple-poplar; *G* willow; *H* oak-hickory.

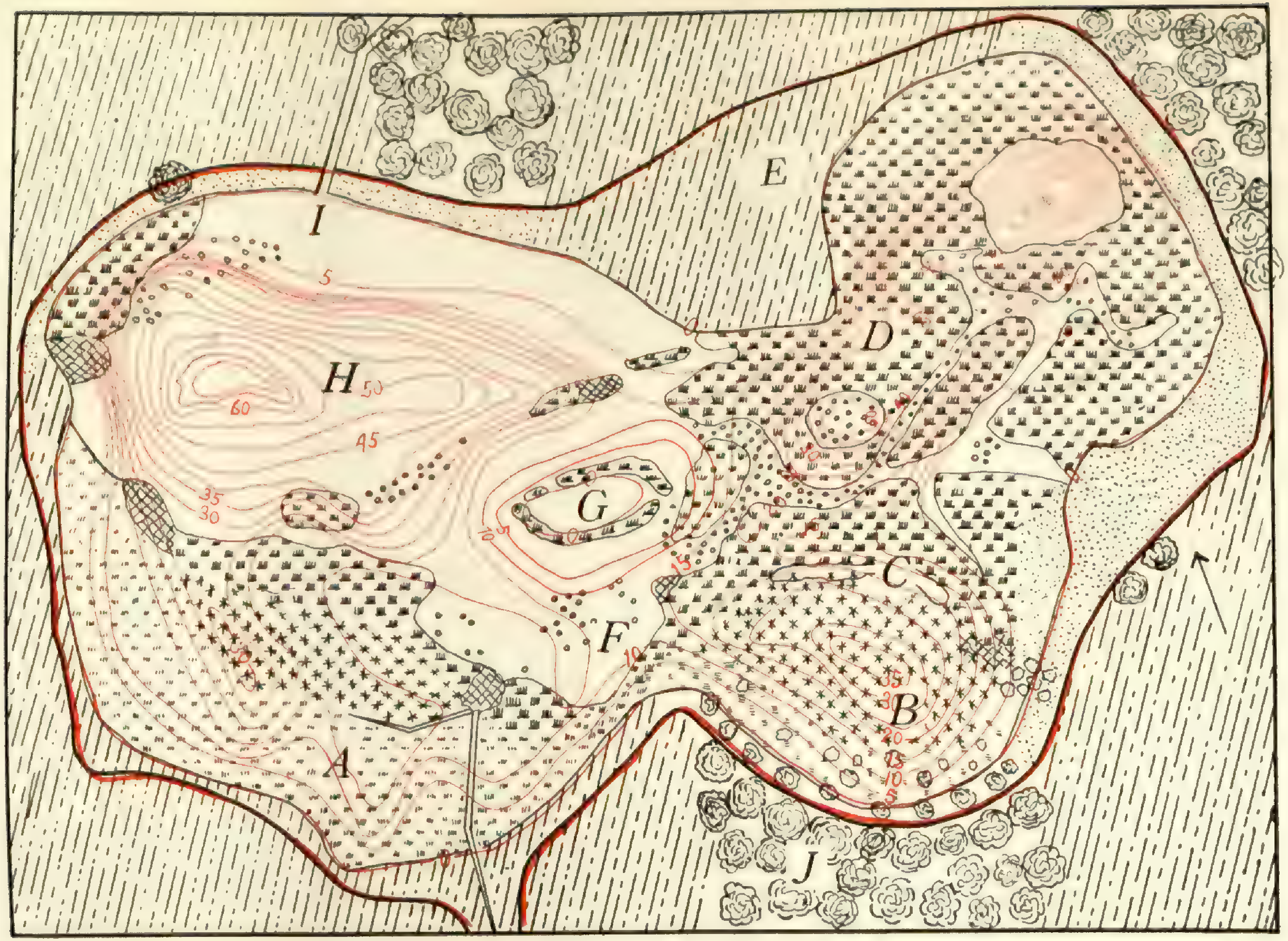

Fig. 3.—Dead Lake. Contours of the bottom of the post-glacial lake in red. The heavy line indicates the position of the shore before drained. The line o indicates the water level when the map was made. Scale 1:4800. Contour interval five feet.

Distribution of plants when the map was drawn in black. *A* area which had been cleared of tamarack before it was suitable for maple-poplar or the clearing society; *B* tamarack; *C* bog shrub; *D* bog sedge; *E* cultivated field; *F* water lilies; *G* island; *H* open water; *I* drain; *J* oak woods.

originally. The volume of water, however, is much smaller than it appears in the figure just referred to, as is seen in a profile through this section of the lake (*fig. 2*). The greatest accumulation of peat is on the western side. The zonal arrangement is also quite different on the two sides. The bog-shrub, tamarack, and maple-poplar zones are almost entirely lacking on the east. On the west, all the zones are present, the tamarack zone being very wide especially in the southwestern portion.

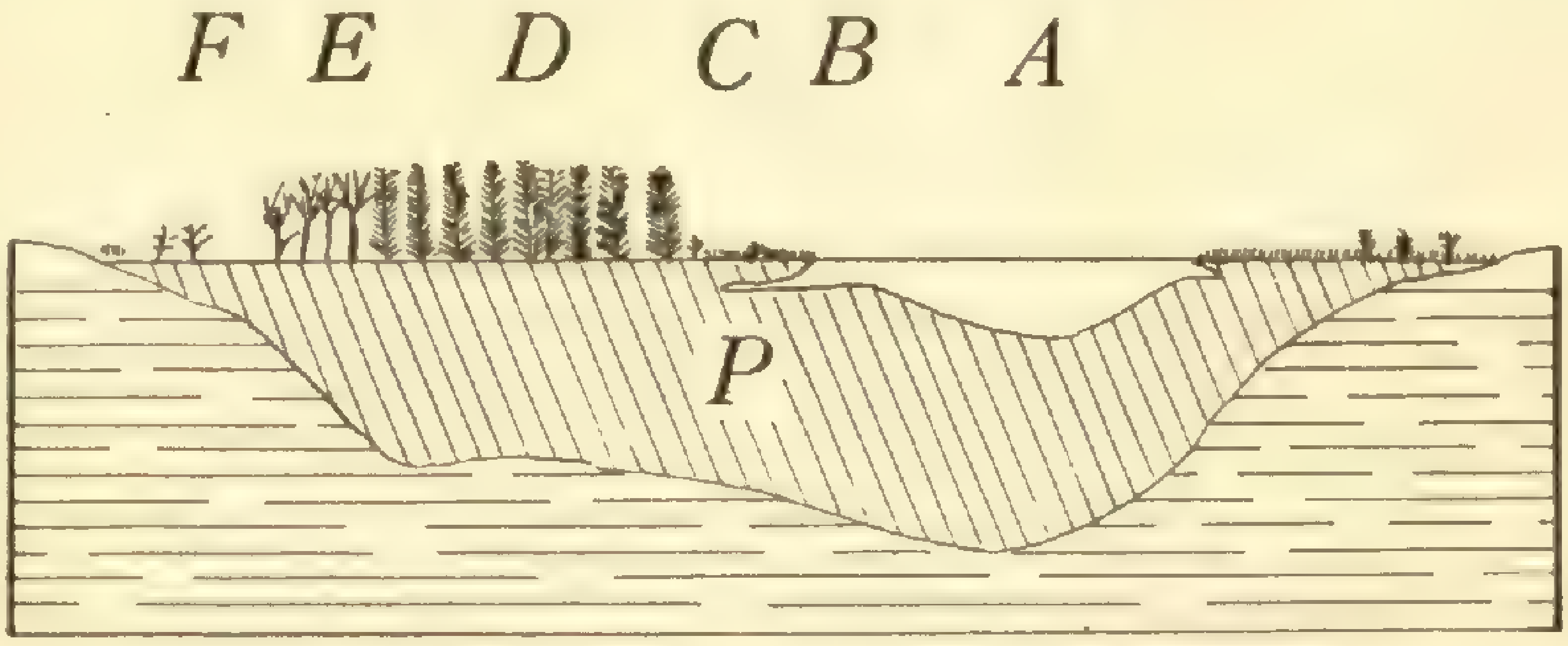

FIG. 2.—First Sister Lake. Profile east and west. *A* open water; *B* bog sedge; *C* bog shrub; *D* tamarack; *E* maple-poplar; *F* willow. Scale: vertical, 1:600; horizontal, 1:2880.

In *fig. 1* it is interesting to observe that the open water now lies over the deepest part of the post-glacial lake; and to follow the variations in the width of the tamarack zone. The southern area is broken by areas of bog shrubs, showing that the tamarack has not entirely captured the area. The northern group, on the other hand, is disappearing, and when a number of trees were cut out for wood a few years ago an entirely different society of plants came in—a clearing society. In other words, conditions favoring the development of a tamarack society are found where the original post-glacial lake was forty feet (12.17$^{\mathrm{m}}$) or more in depth, and where the depth was less than this conditions are favorable for the development of the next zone of plants.

BOG NEAR CARPENTER'S CORNER.—This is a small bog east of Ann Arbor. It is surrounded by high hills on the north, west, and south. On the east a narrow ridge about five feet (1.5$^{\mathrm{m}}$) high separates it from a large "drained swamp." A ditch has been dug through this ridge to drain the bog. The original post-glacial lake was small, occupying about one-tenth of an acre ($400^{sq\,m}$). It had only one basin whose greatest depth was fifty-nine feet (18^{m}). This point was considerably west of the center. The slope of the shore from the eastern margin was very gradual for a distance of nearly one-third the east-and-west diameter, when it becomes very steep. The eastern third of the lake was about fifteen feet (4.57^{m}) deep. The slope from the western shore was much steeper, and hence the greatest amount of water was west of the center.

Today the open water has entirely disappeared. From the banks a group of tamaracks may be seen. These are arranged around a small central area within which are found (**7**) a few individuals of the bog-sedge and bog-shrub zones which formerly occupied large areas. Some of the plants found were *Carex filiformis*, *Sphagnum* sp., *Sarracenia purpurea*, *Cypripedium acaule*, and *Vaccinium Oxycoccus*. Outside of this area is a zone of mixed vegetation. The width varies from several rods to a few feet, the widest area being found on the east. The dominant trees are *Acer rubrum* and *Populus tremuloides*. This area has a rather indiscriminate mixture of bog and lowland plants—it is a tension zone in which conditions are not especially favorable to either group of plants. Around this area and following the shore, is found the marginal area so common to bogs. The plants occupying this area are those usually found in low wet places along rivers.

A comparison of this distribution with borings shows that the central area is over the deepest part of the post-glacial lake. The greatest surface accumulation is on the western side where the lake was comparatively shallow, and over this area *Acer rubrum* and *Populus tremuloides* are the dominant trees.

It is thus possible to tell, with considerable accuracy, the depth of the bottom of post-glacial lakes with one basin by the distribution of the present vegetation. The order of succession is lily, bog sedge, bog shrub, tamarack, and maple-poplar. An island of Cassandra located in a zone of *Carex filiformis* indicates a shallow bottom (**3**), but when it is found in a zone of tamaracks it indicates a deep basin.

DEAD LAKE.[3]—This lake is located about ten miles (16^{km}) north of Ann Arbor. Its longest diameter is nearly directly east and west. Red contours on the map (*fig. 4*) show that the bottom of the post-glacial lake was divided into four basins; a rather shallow ridge running north and south divided it into an eastern and western half, and each half is in turn divided into a northern and southern basin. The central ridge was twelve feet (3.65^m) deep at the lowest point, and in the center it came above the surface, forming an island.

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[3] Mr. FOREST B. H. BROWN assisted in making the borings.

In the eastern half, the northern basin reached a depth of seventy feet (21.33^m) and the southern basin thirty-five (10.66^m) feet. However, a large part of this half of the lake was comparatively shallow. Over a large area the depth was about ten feet (3^m). The other half was also divided into a deep northern basin which reached the depth of seventy-two feet (21.94^m) and a shallower southern basin thirty feet (9.14^m). The greater part of this half of the post-glacial lake was deep. At some time in the past a ditch was dug through the bank on the north and the level of the water was lowered several feet. The conflicting stories told by the older inhabitants make it impossible to determine when this occurred. The vegetation, however, shows that it has been a number of years.

The map of the present distribution of plants at this lake (black parts of *fig. 3*) shows that the peat deposit is largely confined to the south and east. The principal vegetation of the lake is the bog sedge. Only on the south have the tamaracks and the bog shrubs gotten a foothold, though "islands" of these are rapidly spreading over the bog sedge in many places. The absence of the bog flora around the shore of the island in the center of the lake (the vegetation shown on the map is *Scirpus lacustris*), along the northern side of the west half, and on the southeastern corner, is no doubt to be explained in part by the action of the wind, wave, and shoreward push of the ice. However, it must be seen from the map that these places do not stand in a definite relation to the points of the compass. Such vacant places are found where there is shallow water. In just such places the actions referred to above would be most intense. It seems, therefore, that the contour of the bottom rather than the direction of the wind is the controlling factor. The small lake in the northeastern corner is over a very deep basin; the deep western half is for the most part open water. The narrow channels of open water on the eastern portion do not follow the contours but in some places cross them at right angles. Their existence finds its explanation in part in the fact that they are kept open by fishermen who approach the lake chiefly from this side. It is doubtful, however, if this is the entire explanation (**4, 5**). The break in the tamarack zone on the south side is due to two factors. At this point the water was rather shallow and this hindered occupation by bog plants for a long period of years, as has been pointed out; during late years the tamaracks have been cleared away and the place kept open as a watering place for stock. The large open area south of the tamaracks is an area suited for tamarack growth. The tamaracks formerly growing there were removed for wood and poles before the surface had been raised enough to make it suitable for either the maple-poplar or the clearing society. It is occupied chiefly by marsh ferns and sedges, with a few *Rhus venenata*. A narrow border of *Ulmus americana* is found along the southeastern shore (*fig. 4*).

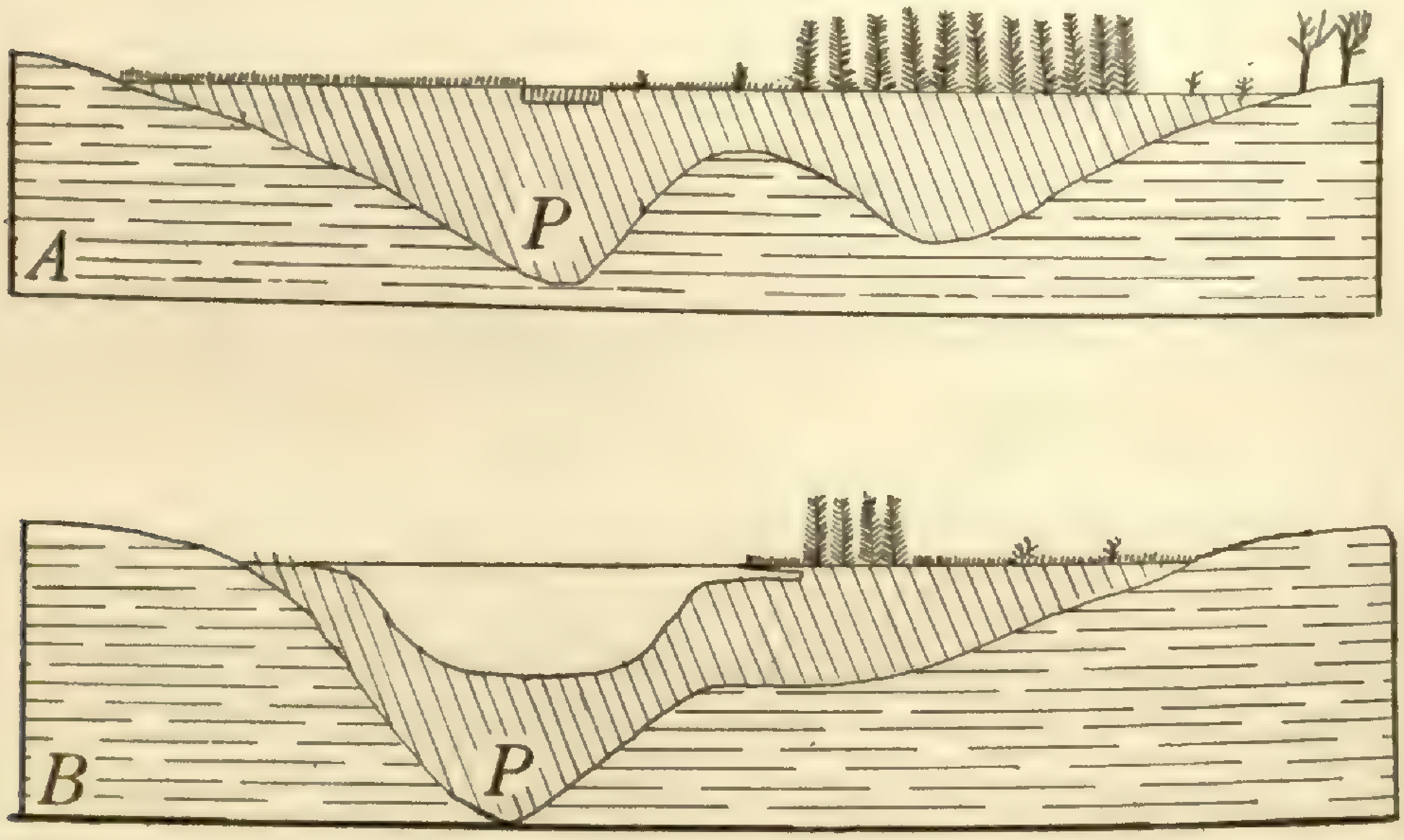

FIG. 4.—Profiles through Dead Lake. *A* through the eastern half; the small body of "open water" is filled with lilies and submerged water plants. *B* conditions in the western part of the lake. Scale: vertical, 1:600; horizontal, 1:4800.

MUD LAKE.—This lake has been described by PENNINGTON (**6**). It was a very large post-glacial lake but has been almost entirely filled with marl and peat. The greatest deposit of peat is on the northern side, and the open water is very close to the southern shore. In entering the bog from the north one passes through a number of large areas of bog shrubs, wholly or partly surrounded by tamaracks. In these areas are sometimes found small patches of tamarack and spruce. A profile was run across the bog, north and south, through these areas and the open water. This shows that the areas occupied by tamaracks are located over shallow places in the post-glacial lake, and that areas of bog shrubs are located over deeper basins. The borings showed that this lake had a number of basins very much the same as found at Dead Lake. It has reached a later stage of development, however; the dominant vegetation is the bog shrub and tamarack.

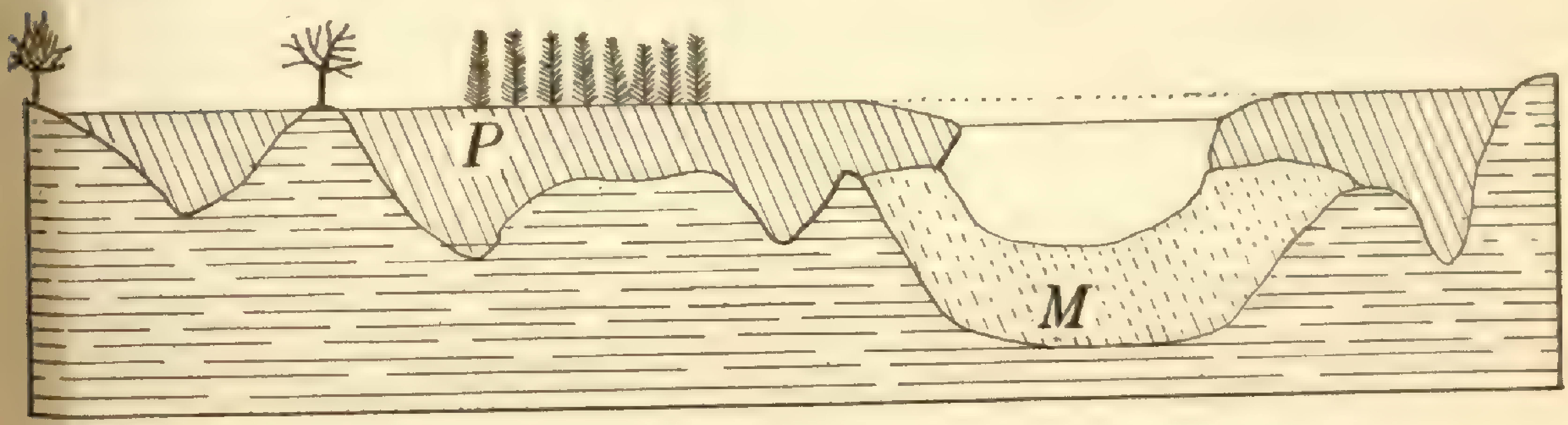

FIG. 5.—Profile north and south through Snow's Lake. The dotted line shows the water level before drained. Scale: vertical 1:300; horizontal, 1:3048.

SNOW'S LAKE.[4]—This lake is located about fifteen miles (24^{km}) west of Ann Arbor. It was formerly a very large lake, but has been almost filled with peat and marl. The bottom of the post-glacial lake was very irregular, as is seen in the profile (*fig. 5*). This profile runs north and south. The deepest and largest basin was near the northern shore; the southern part of the lake was comparatively shallow. A few years ago the lake was drained at the northeastern corner and the level of the water was lowered in the lake. Over the shallow parts of the lake the peat had already become solid, and the draining did not change the level of the surface. Near the open water, however, the plants were still floating, and when the water was drained they sank to the new level. The surface today slants rapidly toward the water; especially is this true for the first few rods immediately next to the open water. It is very surprising from the road to see fine large oak trees growing apparently in the peat bog. However, when one goes over to the oak and examines the soil in which it is growing, the matter is easily explained. These "islands" of oak and other upland trees are not growing in peat, but on one of the islands formed by projections from the bottom of the lake. *Fig. 5* shows such an island with an oak growing upon it.

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[4] A careful study of this lake was made by Dr. JEAN DAWSON, but the results have not been published.

The same relation of present distribution and depth of the original post-glacial lake holds true in lakes with several basins, as it did in lakes with only one: open water over the deepest and largest basins, wide zones of plants where the bottom of the post-glacial lake sloped gradually, a definite order of succession of plant zones. Greater care must be exercised, however, in the determination of depths by the present vegetation, especially in lakes with many small basins just at the time when large areas are beginning to become favorable for the next group of plants. The occupation will take place most rapidly over shallow parts, because here the peat will become firm sooner and the conditions will first be favorable for the next group of plants.

CONCLUSIONS.—The chief factor determining the position of the greatest amount of peat deposit and the width of the zones of plants at the local peat bogs is the depth of the water in the different parts of the original post-glacial lakes. The chief factor in determining the position of the open water is depth; given time enough, the open water will disappear from all our lakes.

In places where the water is very shallow the bog flora is unable to get a start because of the wave-action caused by the winds and on account of the shoreward push of the ice. Such places, however, bear no definite relation to the points of the compass.

Different zones of plants follow in a definite orderly succession; lily, bog sedge, bog shrub, tamarack, maple-poplar.

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POLLINATION IN LINARIA

WITH SPECIAL REFERENCE TO CLEISTOGAMY

E. J. HILL

(WITH FOUR FIGURES)

I. POLLINATION BY INSECTS

The genus Linaria furnishes examples of adaptations to both cross- and self-pollination. Of the sixteen species given in KNUTH'S *Handbuch der Blütenbiologie*, nine are said to be visited by insects and may be pollinated by them. One, *L. origanifolia* DC., as observed by MACLEOD, is adapted to insects, but was not seen to use them. Four or five seem to be restricted to self-pollination, and all can also employ it. Some produce cleistogamous flowers, and as far as these can be of service, are compelled to pollinate in this way. *L. vulgaris* Mill. (as *Antirrhinum Linaria* L.) was the first to be observed and described. This was by CH. K. SPRENGEL in his book on the relations of flowers and insects, published in 1793. It was one of the first with which DARWIN experimented when preparing the material for his work on the effects of cross- and self-fertilization in the vegetable kingdom. An unexpected presentation of vigor in one of two beds of this species, planted for the purpose of determining some points regarding inheritance, led him to trials with this and other plants on the results of pollination.

Linaria is called a mellitophilous genus, since bees are the principal agents in the process, though in some species several other insects, especially Lepidoptera, share in the work. The honey, secreted by glands at the base of the ovary, flows into the spur of the flower, where it is stored and awaits the visits of insects with a proboscis long enough to reach it. It is therefore well adapted to visitors of this kind belonging to the class called Eutropic by LOEW.[1] The two pairs of anthers are placed at different heights, with the slender style and the stigma in the space between. These are brushed by the back of a bee crowding in to get the nectar in the spur, or by the longer proboscis of a lepidopter, and some of the pollen is removed during the operation. That which was left on the stigma of the flowers by the entering and withdrawing of the bees was the extent of pollination as viewed by SPRENGEL. It was an aid to the plant in securing fertilization indispensable in the case of some, but the full significance in the economy of its life was left for others, especially for DARWIN, to show. SPRENGEL clearly describes the process in the text and figures illustrating *Antirrhinum Linaria*,[2] and in reading his book one wonders at the sagacity of the man so far in advance of his time. The relative position of anthers and stigma, coupled with their simultaneous maturing, can also, as stated by HERMANN MÜLLER, lead just as readily to self-pollination, and in the absence of visits by insects makes it the only possible means of fruitfulness.[3] The same relations hold in the case of the smaller flowers of *L. alpina* Mill., which MÜLLER investigated.[4]

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[1] LOEW, Einführung in die Blüthenbiologie 342, 345. 1895.

The common toad-flax of Europe, *L. vulgaris*, has been naturalized in this country, and is most frequently seen along roadways or in waste grounds. Two native species are generally recognized, *L. canadensis* (L.) Dumort. and *L. floridana* Chapm. A third, *L. texana* Scheele, is made by some, but by others is considered a large-flowered form of *L. canadensis*. This seems to be the only one that has been studied with regard to its pollination. It is widely distributed, usually growing in dry locations, such as sandy or rocky ground. Its small flowers ally it more to *L. alpina* than to *L. vulgaris*, and like these it is adapted to pollination by insects. CHARLES ROBERTSON observed the flowers in Florida, and found that they were visited by bees, but more often by butterflies. He says of them: "The spur is very slender and the tube has become so contracted that bees can only insert their tongues, and butterflies cannot suck without touching the anthers and stigma. . . . . The palate, which in *L. vulgaris* permits the visits of bumble-bees only, seems to have lost its function, for it is so weak that it entirely fails to exclude butterflies or even flies."[5] Where I have noticed it in the dune region near Chicago, it does not appear to be very extensively sought by insects, but species of Syrphidae may be seen flitting from flower to flower of this and of plants of *Krigia virginica* in blossom at the same time, perhaps as much in search of pollen as for their sweets.

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[2] SPRENGEL, Das entdeckte Geheimniss der Natur im Bau und in der Befruchtung der Blumen 317. *pl. 17. figs. 5–11, 14, 18, 19.* 1793.

[3] MÜLLER, Die Befruchtung der Blumen durch Insekten 279. 1873.

[4] ———, Alpenblumen 275. 1881.

[5] ROBERTSON, Zygomorphy and its causes. III. BOT. GAZETTE 13:228. 1888.

MÜLLER examined other European species of Linaria with reference to this matter, among them *L. minor* Desf. and *L. arvensis* L. Their flowers are very small, but adapted, like *L. vulgaris* and *L. alpina*, to pollination by bees. As a weed in his garden at Lippstadt he "looked in vain" for visitors to *L. minor*, and *L. arvensis* was repeatedly watched in favorable weather in another station with a like result. Hence he concludes that they are restricted to self-fertilization. As the anthers burst at the same time the stigma matures, should a bee come for the nectar the flowers are ready for cross-pollination. This condition lasts only a short time; the stigma is soon covered with pollen, and self-fertilization is accomplished. Since MÜLLER cannot imagine that a flower, in all the peculiarities of its structure fitted for pollination by insects, should still be very exceptionally visited and crossed by their instrumentality, he concludes that we have in these plants a deteriorating descendant of an ancestor with larger and more striking flowers, in whose pollination bees as a rule took part.[6] He considers that the same is true of various other plants with diminutive or inconspicuous mellitophilous flowers which are now very rarely visited by bees, citing among others *Vicia hirsuta* Koch as a similar case, whose style bears unequivocal marks of arrested development, the brush being reduced to a dozen hairs at most.[7]

II. THE CLEISTOGAMIC CONDITION

It is only a step from this reduction of floral organs mentioned by MÜLLER to flowers so diminutive and constructed in such a way that they do not open at all, or the cleistogamic stage, in which self-pollination is the only means of securing fertility. Of the eight types of entomophilous flowers made by DELPINO, the sixth is that in which the anthers and stigmas are close together and included. Linaria answers these conditions, as must indeed be the case with all cleistogamous flowers in respect of the proximity of the organs essential to fertility. It is these cleistogamous flowers I have mainly investigated. My attention was first called to them in 1905, when flowers of this character were found on *L. canadensis* growing upon the sandstone rocks at Oregon, Ill. They were quite inconspicuous. The minute corolla, when pushed off by the enlarging ovary, showed a faint tinge of violet on its upper margin, the main part being colorless. Since it was the middle of July, all traces of the sterile radical shoots had disappeared, as well as such flowers as are ordinarily found earlier in the season, if, indeed, they had been formed at all. The plants were generally small, the shortest mostly with simple stems. Some were branched, the tallest about 4^{dm} high. Since the species is well represented, though not abundant, on the sand dunes at the south end of Lake Michigan, there has been an opportunity to observe it each season since, and to note the different stages of development. The plants begin to blossom about the first of May and continue, in some form, the production of flowers till the middle or latter part of July, when the heat becomes too trying for them in the dry sand. On the larger plants there is a gradual diminution in the size of the flowers from the earliest, $6–8^{mm}$ long, with a diameter of limb of $8–12^{mm}$, till the cleistogamous stage is reached. In some plants of this character, this may occur in the early part of June. It is exceptional to find flowers which are relatively conspicuous during the later part of the life of the plant, and when found they are apt to be much reduced as compared with the earlier forms. The inflorescence being indefinite, the lengthening of the main stem and branches favors this progressive diminution. Plants that do not exceed 10 to 15^{cm} usually remain simple and are mainly restricted to cleistogamy. Plants taller than this commonly have flowers adapted to pollination by insects, though it must be rare in the smaller flowers, if done at all, when the limb of the corolla is but 3 or 4^{mm} in diameter, as MÜLLER found was the case with the small flowers he mentions.

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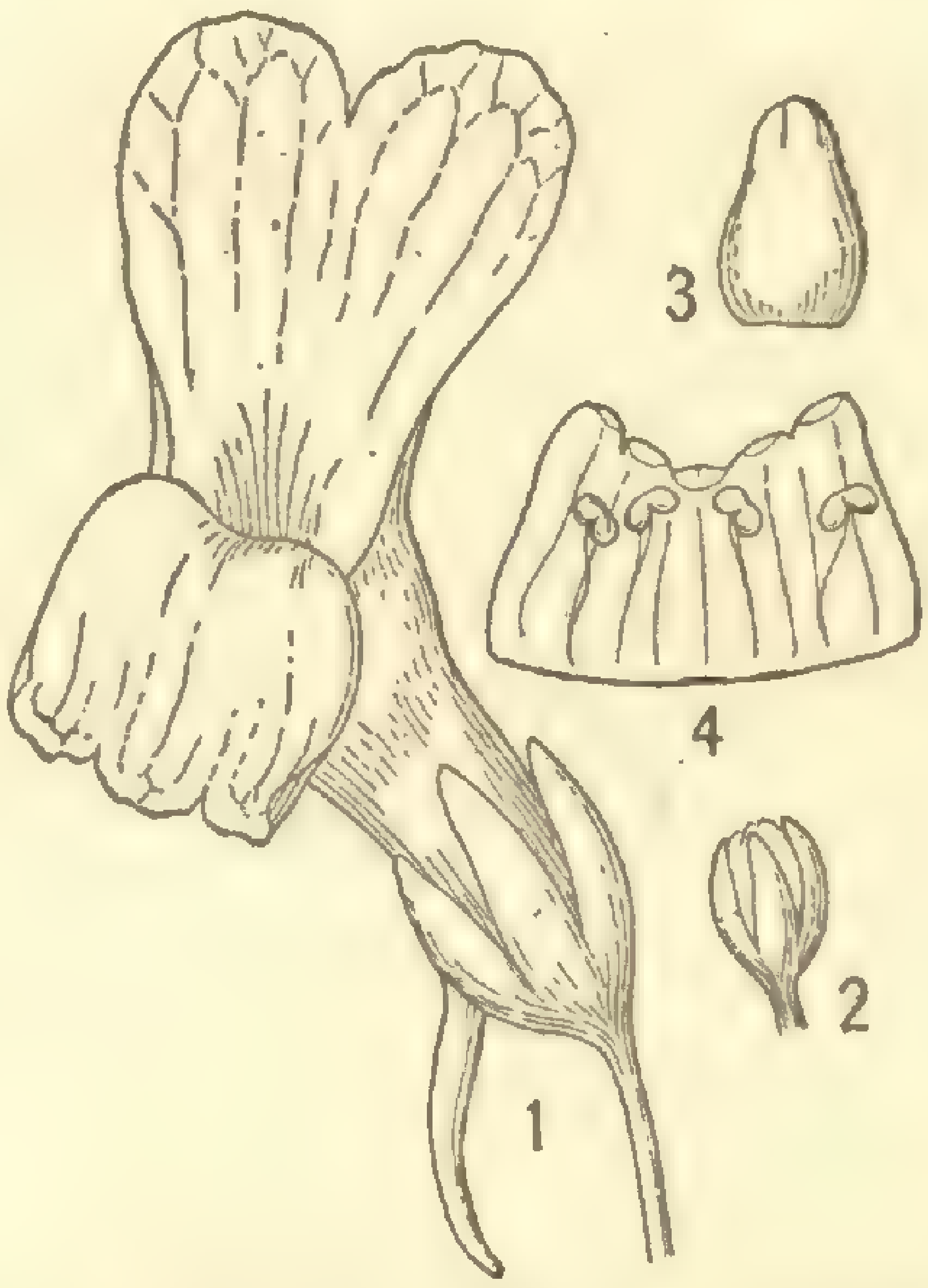
[6] MÜLLER, Weitere Beobachtungen III. Verh. nat. Vereins Rheinl. Westf. **39**:28. 1880.

[7] ———, *Ibid.* II. *Op. cit.* **38**:360. 1879.

Cleistogamy begins on stems not more than 2^{cm} high, which may be limited to a single flower at the tip, or perhaps lengthen enough to bear two or three. Flowers will appear on these diminutive stems as early as the larger petaliferous ones on the vigorous plants, the two forms being synchronous, but on stems under different circumstances. They continue to increase in number on plants of this simple character until the stem ceases to lengthen or becomes mature, various heights being reached, but rarely more than 2^{dm}. Other slender and normally simple stems, usually not flowering at all till 12 to 15^{cm} high, bear as a rule small open flowers, and may continue to do so for some time, growing on till by progressive diminution of size the cleistogamous stage is reached. But the plants are apt to branch when 15 to 20^{cm} high, and bear the larger flowers on the main stem and branches that successively form. Two or three of these stouter stems often spring from the same root, forming a small cluster, with larger and more abundant radical shoots, the plant in all its features showing its greater vigor. In BRITTON and BROWN'S *Illustrated flora*, the statement is made under *L. canadensis:* "A dwarf form with no corolla is frequent." This evidently refers to the cleistogamous form. But the stage with no corolla is not confined to the dwarf plants. It was not on such that I noticed them at first, but on those which varied in height. In the dune region they may rise to 6^{dm} and bear the closed flowers in the later stages of growth. As the taller forms often branch quite freely, great numbers of capsules are borne, developing on the principal stem and branches at the same time and long after the ripened capsules lower down have opened and dropped their seeds. Since the branches ascend rather sharply, frequently rising well up to the level of the primary axis, a copiously branched plant, sometimes with fifteen to twenty members, may result. These have a bushy appearance, but they all produce the closed flowers before the plant dies, and manifest its ability to bear vast numbers of seeds.

The length of the corolla in the closed flowers is 1.2 to 1.6^{mm}. It is tubular, or sometimes slightly funnelform, but owing to the quite rapid growth of the ovary soon becomes enlarged at the base, and when pushed off is shaped more like an inverted funnel; or, if enlarged at the same time above, it has somewhat the form of an hour-glass. The limb is slightly irregular, the two-lobed upper lip being higher than the three-lobed lower, and overlapping it in the bud. In the illustration *fig. 1* shows an ordinary chasmogamous flower, *fig. 2* a cleistogamous flower, both enlarged five diameters, *figs. 3* and

4 a cleistogene corolla enlarged ten diameters, that of *fig. 4* displayed, the division being made between the two lobes of the upper lip. The style and stigma, if represented, would be between the two pairs of stamens as in the ordinary flowers, the stigma in this case closely pressed by the anthers when the parts are in place. The four stamens are apt to be present, and slightly didynamous. Sometimes a small protuberance at the base of the tube represents the spur. In the smaller chasmogamous forms, this may be reduced to a short sack or tooth, and usually decreases in size as the other parts diminish. But in some cases it remains relatively longer in comparison with the lessened tube and limb. I found no case of a cleistogene without a corolla. But as in other cases of cleistogamy it is easy to imagine the flowers represented by the calyx and the essential organs of fructification.



FIGS. 1–4.—*Linaria canadensis.* Fig. 1, petaliferous flower ×5; *fig. 2*, cleistogene flower ×5; *fig. 3*, corolla of cleistogene flower ×10; *fig. 4*, the same, displayed, ×10.

Depauperate as well as larger forms with cleistogamous flowers have been noted by others. RYDBERG, in his *Flora of the Black Hills*, mentions a *L. canadensis* collected at Custer as being "slender and depauperate, apparently with cleistogamous flowers. The same has also been collected in Nebraska."[8] The month given for RYDBERG'S collection is August. J. R. WEBSTER records cases observed by him at Milton, Mass., August, 1898. The plants were again noticed the next year, being "examined almost daily from April to October, and were seen to produce flowers abundantly which were all cleistogamous." They were observed by him in other localities, in which were also racemes which bore in addition fully developed flowers.[9] As the plants at Milton are said to reach the height of twenty to twenty-four inches and to produce branched racemes, "some of which were a foot or more in length," they were evidently of the larger forms, such as grow in the dune region in Indiana. But in their lack of chasmogamous flowers, they are somewhat different from any I have noticed there. The cases alluded to in his article as seen in "other localities" are more like those I have described. T. S. BRANDEGEE has likewise observed the plant about San Diego, Cal., "bearing cleistogamous flowers on the lower part of the main and the whole length of many side branches,"[10] apparently more like the larger forms here. Yet these statements from different sources indicate that the plant varies somewhat in its behavior in the respective localities, due perhaps to different environment.

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[8] RYDBERG, P. A., Contrib. U. S. Nat. Herb. 3:517. 1896.

[9] WEBSTER, J. R., Cleistogamy in *Linaria canadensis.* Rhodora 2:168. 1900.

Cleistogamy in Linaria is not confined to our wild toad-flax. It is one of the forty-four genera given in an article by KUHN in 1867 as producing examples with flowers of this character.[11] This list has been much increased since that date. KUHN does not give the name of the species, but probably refers to *L. spuria* Mill., whose peculiar florescence was described by EUGENE MICHALET in 1860.[12] MICHALET gives it as an example of a plant bearing hypogeous flowers. "These flowers," says DARWIN, "may be ranked as cleistogamic, as they are developed, and not merely drawn, beneath the ground."[13] It also has another peculiarity, according to MICHALET "infrequent in an annual plant," that of producing hypocotylous buds. Its lower leaves are opposite and much crowded. Two kinds of branches spring from their axils. Some of these, strong and often much elongated, spread over the surface of the ground; others short, slender, and much twisted, with small squamose leaves, gather in a bunch above the collar of the root, "all with a manifest tendency to bury themselves in the ground, especially the small hypocotylous branches which sometimes appear." Under suitable conditions they may penetrate the ground to the depth of 2^{cm}. On account of the pressure to which they are subjected, the flowers are poorly developed, but otherwise show nothing peculiar in their structure. The corolla is crumpled and deformed, but "preserves even its natural color, with the two brown spots on its upper lip." The calyx alone loses its color. Fructification takes place regularly. MICHALET adds that the phenomenon can be produced at will by heaping earth around the lower part of the plant, this not interrupting the flowering of the covered portion. The treading of cattle and the pressure of wheels bring about the same result. As this plant of Europe and northern Africa is now introduced into this country, being, according to GRAY'S *New manual*, "occasional on ballast or waste grounds," an opportunity is provided for observing its behavior here. Another species of north Africa, *L. agglutinans* Pomel. var. *lutea*, belongs to this class of hypogeous plants, as observed by L. TRABUT in Algiers. It has cleistogamous flowers on shoots which spring from the stem near its base and ripen their fruit underground.[14]

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[10] BRANDEGEE, T. S., Cleistogamous flowers in Scrophulariaceae. Zoe **5**:13. 1900.

[11] KUHN, M., Einige Bemerkungen über Vandellia und der Blütenpolymorphismus. Bot. Zeit. **25**:67. 1867.

[12] MICHALET, E., Sur la floraison des Viola . . . . et du *Linaria spuria*. Bull. Soc. Bot. France **7**:465. 1860.

[13] DARWIN, C., Different forms of flowers 325. 1877.

III. RELATIVE ADVANTAGES OF THE TWO MODES

It is a distinct advantage to a plant growing under the conditions of *Linaria canadensis* to prolong its period of fruiting with a lessened demand on its supply of food. The environment is xerophytic. At Oregon it was the southern slope of a steep hill, fully exposed to the light and heat of the sun. The soil was sandy, and soon parted with any moisture that was supplied by rains and dews. The conditions in the dunes are similar, the slopes of sand hills or along paths and roadways in open sunny spots. The growth is usually scattered, though many plants may form a community, but the ground is not covered with a dense mat or bed as it commonly is by *L. vulgaris.* The slender stems provide but meager shade for the ground about their roots. In the early part of the season, or if it continues wet, the radical shoots form rosettes around the base of the stems, which protect the roots to some extent. In ordinary seasons these soon wither, and they may not be formed at all on plants which spring up later, being minute or wanting as in the smaller early plants. It is also a species poorly adapted to competition. When pressed by perennials, or by plants disposed to form a close stand, it soon disappears. And the plants associated with it, even if perennials, are not very sturdy competitors, but mostly of gregarious habit also. At Oregon they were chiefly *Lechea tenuifolia, Talinum teretifolium, Selaginella rupestris, Silene antirrhina divaricata;* in the dunes of Indiana, *Krigia virginica, Arabis lyrata, Viola pedata, Polygonella articulata,* and *Festuca octoflora.* But to whatever extent the time of fruit-bearing may be prolonged by cleistogamy, it is comparatively short in such habitats. It starts early, when there is little competition, and being an annual or fall-biennial, soon accomplishes its life-work.

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[14] KNUTH, Handbuch der Blütenbiologie 32:113. 1905.

That the cross-pollination of the earlier and larger flowers of *L. canadensis* must also be much to its advantage, in increase of vigor and productiveness, is evident from the nature of this process. This was clearly proven by DARWIN in his experimental work with cross- and self-fertilized plants. Of two beds of *L. vulgaris,* raised respectively from self-fertilized and crossed seedlings, those of the latter were seen to be much more vigorous. This led him to trials with this and other plants, the results of which are given in his book upon this subject. The case of Linaria needs only to be cited. As showing the vigor, "the naturally crossed plants were to the spontaneously self-fertilized plants in height, at least as much as 100 to 81." In regard to fruitfulness similar results came from the two modes of treatment, that of allowing or preventing the visits of bees. "The number of seeds in the capsules on the exposed plants to the average number in the finest capsules on the protected plants was as 100 to 14," or as expressed by him in a summary of plants so treated, the self-fertilized were "extremely sterile."[15] KNUTH is even more emphatic in stating that though self-pollination is possible and can occur spontaneously in *L. vulgaris,* it is of little consequence or without result.[16] In cases of this kind, where pollination from without and within takes place simultaneously, HERMANN MÜLLER thinks it probable that the former preponderates in its effects, and that the desired result is secured in this way.[17]

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[15] DARWIN, C., Cross and self-fertilization in the vegetable kingdom 88, 89, 363. 1877.

[16] KNUTH, Blumen und Insekten auf dem nordfriesischen Inseln 111. 1894.

[17] MÜLLER, Befruchtung der Blumen 279.

IV. LIGHT AND HEAT AS FACTORS IN CLEISTOGAMY

The behavior of *Linaria canadensis* led to the conclusion that the gradual diminution in size of flowers was connected with the increase of heat, and perhaps of the light, to which they are exposed. Taking the larger plants as typical examples, the two features are in inverse proportion. This might be taken as a coincidence, but it seemed to be explained better as a coordination, and more in harmony with observations and experiments by others. In 1874 BOUCHÉ called attention to his observations that the diminution in the size of flowers and the production of cleistogamy depend in some plants on the decrease or increase of heat, in others on the decrease or increase of the length of the day. In the behavior of some, of which *Vinca rosea* L. is an example, the light acted favorably, the largest flowers being formed during the longest days, the smallest during the season of the shortest days. This seemed to depend on the light, since with a higher temperature after the longest days had gone by the decrease went on. In other cases cited by him, the decrease in size and production of cleistogamy are coordinated with the increase of heat and light, as if these acted unfavorably. As examples of this are the malvaceous plants, *Pavonia hastata* Spr. and *P. praemorsa* Willd. They begin to bloom at the end of May and show the phenomena of diminution and cleistogamy until the autumnal equinox, after which the flowers gradually increase in size till the beginning of winter or close of their floral season.[18] The case of the pavonias more closely accords with that of *L. canadensis*, as far as the floral season of the two coincide. But since, according to BOUCHÉ, the effects are not uniform, and may even lead to opposite results with different plants, there must be something in the plants themselves which causes the different response, or other environmental conditions must be taken into account. In the case of Linaria, I had associated it chiefly with the increase of heat which ordinarily occurs in summer, and the consequent diminution or more rapid removal of the moisture from the soil of such localities as the plants frequent. The equilibrium between absorption, either from the air or ground, and transpiration is disturbed. The smaller or cleistogamic flower, requiring less food, permits a husbanding of resources for the production of seed.

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[18] BOUCHÉ, Gesells. naturf. Freunde 90, 91. 1874.

The vitality of the plant is lessened, but its ability to bear seed in abundance still remains. Economy in productive power results in a prodigality of the means to perpetuate. The waste, seeming or actual, is seen in the countless numbers of seeds which never have a chance to germinate. The scattered plants which annually appear show the need of this productiveness in order to obtain a few that can overcome the adverse conditions.

Aside from any effect which the increase of heat and light may have upon a plant in augmenting transpiration, and thereby making it advantageous to diminish the exposed surface, it is plain that the essential organs of reproduction are withdrawn from such effects far more in cleistogamy than in chasmogamy. As the name implies, these organs are hidden. But there is also a further tendency in many cases of cleistogamy to withdraw the perianth, or protective organs, from the direct effect of the sun's rays. *L. canadensis* is an example of the former tendency, *L. spuria* and *L. agglutinans* of the latter. These two species, as already stated, bend their peduncles down to produce their flowers or perfect their fruit beneath the surface of the ground. Other well-known examples of this are the milkworts, *Polygala polygama* Walt. and *P. paucifolia* Willd., bearing their flowers of this kind on subterranean runners. In the violets, where cleistogamy is so prevalent, the peduncles of the summer (usually apetalous) flowers are generally much shorter than those of the large petaliferous blossoms in spring. The flowers are more or less withdrawn from the light and shaded by the much enlarged leaves of the summer growth, or they may be borne on stems so shortened or declined as to be hidden under fallen leaves or buried in soft humus. The production of the closed flowers under such conditions may be due to a diminished intensity of light, as far as this has a bearing on them. Experiments like those of VÖCHTING show that the perianth of flowers is affected by decrease of light more than the reproductive organs. Chasmogamous flowers may be made cleistogamous in this way. The violets are quite variable in their relations to light, many of them being on the borderland between shade-loving and light-loving plants. The majority of our wild species bear their petaliferous flowers in the earlier part of their season of activity, those of the woods before they are strongly shaded by the leaves of the trees and the taller plants of the forest floor, those of the field or open places before the grass or other growth overtops them. Their period of cleistogamy occurs when they are not subject to the strongest light. The one exposed to the greatest intensity of light, *Viola pedata* L., differs from most members of the genus in not having such flowers. Its season of blooming as well as environment correspond to those of *L. canadensis* when bearing its largest flowers. As a perennial, the violet has the advantage of drawing upon a supply of food stored in its much thickened rootstock. When this is diminished or too much exhausted, it goes on with the production of the enlarged summer-leaves, and by them elaborates another supply of food for storage. This may be a good explanation of its lack of the cleistogamy so general among its kindred, since it does not seem adequate to the work of bearing flowers and perfecting seed while producing the food for the future need of a xerophytic perennial. Under diminished temperature and favorable conditions of moisture its work of bearing petaliferous flowers may be resumed in late summer and autumn, but they are mostly smaller and much less developed than those of spring. *V. lanceolata* L. is also a species frequent in our dune region. It is a light-loving plant, often greatly exposed in the open sandy border of sloughs, but being hygrophytic has a supply of moisture on which to draw. Hence it passes its summer stage in the production of cleistogamous flowers, which continues long after that of the petaliferous has ceased. Yet it partakes of the general tendency among the violets, that of bearing them on shorter, more hidden stems, with the additional habit of producing them on stolens close to the ground. But *L. canadensis*, being an annual subject to xerophytic conditions, cannot draw on such resources as these two violets have. The development of its cleistogamous flowers evidently depends on its relations to heat and moisture more than on those of light.

V. DEGENERACY IN FLOWERS OF LINARIA

In *L. canadensis* is found an example of a plant passing through decadent stages to the condition of cleistogamy. The slight irregularity of limb and the occasional remnant of a spur show degeneracy, even if the smaller and varying intermediate forms of flowers were not present. It has already been stated that MÜLLER looked upon *L. minor* and *L. arvensis*, and small-flowered species of Vicia, as examples of plants which had descended from those adapted by their floral structure to pollination by insects. In the plant we are considering, this process is epitomized. Pollination by the help of insects takes place in flowers of an inflorescence which gradually undergoes such changes in a single season as to preclude it. The process of reduction is seen in actual working, and it may be that such flowers, rather small at best, are on the way to a stage where visitation by insects will cease. Yet one cannot regard the explanation as entirely valid. By the very principle of adaptation here invoked, the opposite might come true; that is, visits by insects, frequently repeated and continued for a long period of time, would finally produce flowers better suited to their work. Irregularity of floral structure is regarded as such an adaptation, and to some extent has been explained by it. A causal relation between the two is traced. In DARWIN'S list of genera with cleistogamic flowers, thirty-two of the fifty-five he gives have the flowers in their most advanced stage irregular. He says that this "implies that they have been especially adapted to fertilization by insects."[19] Without pressing such explanations too far, it is seen in the case of the wild toad-flax that provision for cross-fertilization is made in the structure of flowers borne simultaneously with the cleistogamous, or at an earlier date, on the same plant. In this there is insured to the species the present means of invigorating its life, the primary benefit to be derived from it, whether it be a waning or waxing advantage.

CHICAGO

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[19] DARWIN, C., Different forms of flowers 339.

CURRENT LITERATURE

MINOR NOTICES

Botanical expedition to southern Brazil.[1]—The recently published volume on the results of the botanical expedition of the Royal Academy of Science of Vienna to southern Brazil in 1901 contains an account of the Pteridophyta and Anthophyta by Professor R. VON WETTSTEIN in collaboration with several prominent specialists. The conditions under which the expedition was undertaken, the personnel of the exploring party, the detailed itinerary, and the general physical features of the country visited are briefly set forth in the *Einleitung* and *Reisebericht*. The major part of the volume embodies the taxonomic results of the expedition; the larger families treated and the cooperating botanists are as follows: the Filicineae by H. CHRIST, Orchidaceae by O. PORSCH, Gramineae by E. HACKEL, Melastomaceae by C. RECHINGER, Cyperaceae by E. PALLA, Malpighiaceae by C. KRALIK, Bromeliaceae by C. MEZ, Sapindaceae by L. RADLKOFER, Verbenaceae by A. VON HAYEK, Amarantaceae by A. HEIMERL, Gesneriaceae by K. FRITSCH, and the Eriocaulonaceae by W. RUHLAND. Several smaller families are also included. More than 1300 species are recorded from the various groups thus far elaborated, and of this number nearly 100 are new to science.

The new species are fully characterized, and the descriptions are mostly in Latin; the author of the Cyperaceae, however, has unfortunately chosen to describe the new species of this family in German, thus marring somewhat the uniformity of the work as a whole. The text is supplemented by numerous illustrations, and certain orchids are beautifully portrayed in color. The publication represents the work of eminent specialists and forms a reliable and valuable addition to the taxonomic literature pertaining to the flora of South America.—J. M. GREENMAN.

Vegetation of Java and Sumatra.—The first and second parts of the seventh series of KARSTEN and SCHENCK's now well-known *Vegetationsbilder*[2] is devoted to a dozen plates (with descriptive text) representing the plants of the volcanic regions of Java and Sumatra, and especially the reoccupation of those areas which have been at one time or another devastated by the erupted solid, liquid, or gaseous materials. Among others are three views from Krakatoa. This section by Dr. ERNST sustains the high standard of the work.—C. R. B.

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[1] WETTSTEIN, R. VON, AND SCHIFFNER, V. Ergebnisse der botanischen Expedition der kaiserlichen Akademie der Wissenschaften nach Südbrasilien 1901. I. Band. Pteridophyta und Anthophyta unter Mitwirkung zahlreicher Fachmänner herausgegeben von R. VON WETTSTEIN. Erster Halbband. Denkschr. Math.-Nat. Kl. Kais. Akad. Wiss. **79**:1–313. *pls. 26. 1 map. figs. 12.* 1908.

[2] KARSTEN, G., AND SCHENCK, H., Vegetationsbilder. 4to. VII. Reihe, Heft 1, 2. ERNST, A., Die Besiedelung vulkanischen Bodens auf Java und Sumatra. *pls. 1–12.* Jena: Gustav Fischer. 1909. *M5.*

NOTES FOR STUDENTS

Inheritance of sex.—CORRENS[3] has continued his studies on gynodioecious plants in order to discover what determines the sex of the flowers on the gynomonoecious individuals, and the sex of the two classes of individuals belonging to such species. He finds that the curve of frequency of hermaphrodite flowers in *Satureia hortensis*, instead of presenting two modes, as previously reported by him, one in the mid-season and one at the end of the season, has only a mid-season mode. The mode which appeared at the end of the season was due to the repeated counting of flowers which remained open more than one day.

During the middle of the season no flowers open on the second day, but late in the season the petals seem to be more resistant, and climatic conditions are less severe, so that the same flowers were unwittingly counted several times. When each flower is marked as it is counted, it is found that the proportion of hermaphrodite flowers continues to fall till the end of the season.

He also tested the effect of environmental conditions upon the percentage of hermaphrodite and female flowers produced on plants of Satureia from day to day, and noted the position occupied by each kind of flower on the plant. The results show that poor nutrition, whether the result of poor soil, insufficient illumination, or disadvantageous position on the plant, lessens the proportion of hermaphrodite flowers, and under the combined influence of both poor soil and poor light, only 13 per cent. of hermaphrodite flowers were produced as compared with 79 per cent. produced under normal conditions of culture. However, the general features of the curve of frequency of the hermaphrodite flowers remain the same. With high nourishment the curve for the hermaphrodite flowers falls much more gradually toward the end of the season, though during the early part of the season it is not essentially modified.

It was found that different strains of Satureia show marked differences in the actual percentage of hermaphrodite and female flowers, but that in each case the general features of the curve of frequency are the same. The conclusion is reached that whether hermaphrodite or female flowers are to be produced by a gynodioecious individual is dependent upon nourishment in its widest sense. The same general results may be demonstrated in Geranium, *Silene inflata* and *S. dichotoma*, *Plantago lanceolata*, Scabiosa, Knautia, and Echium.

DARWIN had observed that a single hermaphrodite plant of *Satureia hortensis* was "rather larger" than the female plants of the same species, and in an earlier paper CORRENS had apparently substantiated this observation, without realizing the possibility that some of the plants classed as female might be hermaphrodite plants, rendered *apparently* female by poor nutrition. He undertook to determine the relative weights of these two classes of plants with a more careful analysis of the material. The results show that there is no difference in weight between the female and gynomonoecious plants, and therefore the difference in weight which was assumed by DARWIN to be a secondary sexual character has no such significance.

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[3] CORRENS, C., Weitere Untersuchungen über die Geschlechtsformen polygamer Blütenpflanzen und ihre Beeinflussbarkeit. Jahrb. Wiss. Bot. **45**:661–700. *figs. 11.* 1908.

CORRENS has also investigated[4] the percentage of female and hermaphrodite plants in *Plantago lanceolata* under conditions of controlled pollination, and has shown that while this plant, like Satureia and Silene, shows a marked tendency for each sex to reproduce its own kind, nevertheless there is considerable variation in this regard in individuals of both sexes. By pollinating the same female individual with different hermaphrodite individuals, and by pollinating different females with pollen from the same hermaphrodites, it was shown that the proportion of hermaphrodite offspring and of females is so related in each case that they may be readily calculated, after once the strength of the hermaphrodite tendency in the pollen-parent and of the female tendency in the pistil-parent is known. In other words, each individual appears to have a different strength of these two sex-tendencies and to produce germ-cells of two kinds with respect to these tendencies, the number of each kind of germ-cells produced being perhaps roughly proportional to the strength of the sex-tendencies in the parents.

The theory that the germ-cells of *Plantago lanceolata* do not themselves vary in their tendency to produce a certain sex, but that they are definitely either female or hermaphrodite, puts these plants into the class known as ever-sporting varieties, and makes this paper also a valuable contribution to the study of this recognizedly difficult type of inheritance.

The assumption that each germ-cell is definitely female or hermaphrodite and that the female is dominant allowed the prediction of the actual numbers of each sex produced in the different experiments with a fair degree of accuracy.

Several other papers have recently appeared dealing with the question of sex-determination. DONCASTER and RAYNOR[5] found that in crosses between *Abraxas grossulariata*, a common English moth, and its rare variety *lacticolor*, reciprocal crosses are not equal, for when a *lacticolor* female is crossed with a *grossulariata* male, no *lacticolor* offspring are produced, and males and females are all *grossulariata;* but when the reciprocal cross is made, all of the females are *lacticolor* and all of the males *grossulariata*. To explain this strange situation the authors assumed that sex is a Mendelian character, and that the *lacticolor* character is coupled with the female determinant. It was assumed that both male and female individuals are heterozygous with respect to sex. In this regard their interpretation differed fundamentally from that of CORRENS, who assumed that in the case of *Bryonia alba* × *dioica* and other dioecious plants the female sex is homozygous, and the male heterozygous.

BATESON and PUNNETT,[6] in discussing DONCASTER'S results, show that a simpler explanation may be given by assuming that the male is homozygous and the female heterozygous with respect to sex, and that there is a repulsion between the determinant for the *grossulariata* character and that for the female sex. These assumptions fit all of the facts brought to light in the crosses of Abraxas. This point of view has been briefly restated by DONCASTER[7] in a report to the Evolution Committee of the Royal Society, where a summary of the matings and their results is given. Another case has been reported which seems to correspond very closely with that of Abraxas. The "cinnamon" canaries, i. e., those having plumage of a brownish tint, have pink eyes when hatched. The green canary has black eyes. Misses DURHAM and MARRAYAT[8] have found that when a pink-eyed hen-canary is crossed with a black-eyed cock, all the young of both sexes are black-eyed. The reciprocal cross shows all the male offspring black-eyed, while all the pink-eyed offspring are females, though a few black-eyed hens may occur. The latter are as yet unexplained, but there seems to be little doubt that this cinnamon canary will find an explanation essentially like that given for Abraxas.

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[4] CORRENS, C., Die Rolle der männlichen Keimzellen bei der Geschlechtsbestimmung der gynodioecischen Pflanzen. Ber. Deutsch. Bot. Gesells. **26a**:686–701. 1908.

[5] Proc. Zoöl. Soc. **1**:125. *pl. 1.* 1906.

[6] Science N. S. **27**:785. 1908.

Great advances have likewise been made in the study of the determination of sex from the cytological side, mainly through the work of MCCLUNG, STEVENS, MORGAN, WILSON, and their students. In nearly one-hundred species of insects belonging chiefly to the Hemiptera and Coleoptera, it has been found that there are definite chromosomal differences between the male and female, and that the odd chromosomes, or "accessory" chromosomes as they were called by MCCLUNG, are so distributed at the time of the reduction division that all the female germ-cells are alike, while the male germ-cells are of two kinds. The chromosome group of one of these two types of male germ-cells is like that of the egg-cell, and when such a sperm fertilizes an egg, a female zygote is produced. The other type of sperm has a chromosome group unlike that of the egg, and fertilization with such a sperm produces a male zygote.

An excellent résumé of this work and a discussion of the entire problem of sex-heredity is given by WILSON,[9] who has been most prominently engaged in these new discoveries. Showing how experimental breeding and cytology supplement each other, WILSON lays emphasis upon the necessity of bringing different methods of scientific investigation to bear upon difficult scientific problems like this, and the undesirability of depending upon any single method. In this day of intense specialization this is more fundamental than ever before. Similar cooperation would even improve general discussions of a subject which is being developed simultaneously by different methods, for it has become difficult for anyone to give an adequate treatment of such a subject. WILSON'S discussion would have been rendered simpler and more cogent, if he had grasped the logical homologies between plants and animals now generally accepted by students of genetics. He does not seem to appreciate the fact that it is the *gametophyte* of plants which finds no clear homologue in animals, and so fails to assign a proper degree of importance to the parallelism between the sporophyte and the animal body or soma. Again, if he had been more familiar with the most recent developments of Mendelian theory he would have found that the discoveries in these insects are in perfect accord with Mendelian heredity. Instead of this, he presents as a "naïve assumption" what is now generally held by the students of Mendelism, and known as the "presence and absence hypothesis," the assumption being that the heterozygote and the positive homozygote differ from each other in that the former has an unpaired unit, X, and the latter a pair of units of the same kind, XX.

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[7] DONCASTER, L., On sex-inheritance in the moth, *Abraxas grossulariata* and its var. *lacticolor*. Reports to the Evolution Committee 4:53–57. 1908.

[8] DURHAM, F. M., AND MARRYAT, D. C. E., Note on the inheritance of sex in canaries. Reports to the Evolution Committee 4:57–60. 1908.

[9] WILSON, E. B., Recent researches on the determination and heredity of sex. Science N. S. **29**:53–70. 1909.

CASTLE[10] takes up this question and shows the perfect agreement between the results of these cytologists, and the requirements of the presence and absence hypothesis in Mendelian heredity. In CASTLE'S exceedingly clever discussion an attempt is made to harmonize the apparently antagonistic results with Bryonia, the Hemiptera, and Coleoptera on the one hand, and those with Abraxas and the cinnamon canaries on the other, by assuming that in all cases the female possesses one more unit than the male, this unit being called by WILSON the "X-element." Bryonia, and all of the insects whose male germ-cells have been found to be of two kinds, represent a condition in which the male is a heterozygote, and the female is a *positive homozygote*. CASTLE calls this a "dominant female," but this is obviously a misleading terminology, for if the female were *really dominant* the heterozygote would also be a female and there could be no males. In Abraxas, and the cinnamon canaries, and, as suggested by CASTLE, perhaps also in the pheasant, the female is heterozygous and the male is assumed to be a *negative homozygote*, i. e., wholly lacking the X-element. This is the most promising attempt yet made to bring all the recently discovered facts of sex-heredity in dioecious animals and plants under a single hypothesis.

CASTLE attempts further, by an extension of the same hypothesis, to account for the fact that male animals usually possess more characters than the female. He supposes that these added male characteristics are associated with or produced by a Y-element, the "synaptic mate" of the X-element. He also suggests that progressive evolution may have taken place by the appearance and development of such a "synaptic mate" for the X-element, but this, and also the attempt to explain orthogensis on the same basis, is carrying hypothesis rather far from empirical knowledge.

There can be no question that the problems of sex possess many intricacies and difficulties yet to be solved, but the results of these investigations both from the experimental and the cytological side have placed these problems on a new basis, and opened up many possibilities and suggestions for their further investigation. All of the results seem to point to the truth of the view that sex is predetermined in the germ-cells, and that therefore it cannot be modified by environmental conditions except, of course, by such conditions, as yet unknown, as are capable of producing mutations.—GEORGE H. SHULL.

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[10] CASTLE, W. E., A Mendelian view of sex-heredity. Science N. S. **29**:395-400. 1909.

Current taxonomic literature.—N. L. BRITTON and J. N. ROSE (Jour. N. Y. Bot. Gard. **9**:185–188. 1908) have proposed a new genus (*Carnegiea*) of the Cactaceae. The genus is based on the well-known *Cereus giganteus* Engelm., and contains but the one species. H. PITTIER (Contr. U. S. Nat. Herb. **12**:171–181. 1909) has published 8 new species of flowering plants from tropical America. The descriptions are supplemented by two full-page illustrations and several text-figures; the types are deposited in the U. S. National Herbarium. A. THELLUNG (Bull. Herb. Boiss. II. **8**:913, 914. 1909) records 3 new varieties of *Lepidium pubescens* Desv. from South America. F. STEPHANI (*ibid.* 941–972) has published 43 new species of the genus Mastigobryum from various localities. G. BEAUVERD (*ibid.* 986–988) has published a new Eriocaulon from Brazil and also a new species of Tulbaghia from the Transvaal; the same author (*ibid.* 993–1007) records 8 new species and one variety of Nothoscordum from Uruguay and gives an analytical key to the Uruguayan species. E. G. PARIS (Bull. Soc. Bot. France IV. **8**:Mém. 14, pp. 1–66. 1908), under the title *Florule bryologique de la Guinée française*, has published 6 new species of mosses. F. GAGNEPAIN (*ibid.* Session extr., pp. xxxvi–xliii) has published 4 new species of Zingiberaceae and a new genus (*Ataenidia*) of the Marantaceae from Africa, and also a new species of Calathea native of Indo-China. G. BONATI (*ibid.* 509–515, 537–543) describes 25 new species and 4 new varieties of scrophulariaceous plants from Indo-China. F. GAGNEPAIN (*ibid.* 521–527, 544–548) has published 12 new species of Asiatic plants belonging to the Bixaceae and Pittosporaceae. F. KRÄNZLEIN (Fedde Rep. Nov. Sp. **6**:18–23. 1908) publishes 8 new species of Orchidaceae from Bolivia. WOLFF (*ibid.* 24) records a new Eryngium from Bolivia. O. BECCARI (*ibid.* 94–96) records 4 new species of palms from the Antillean region. W. WANGERIN (*ibid.* 97–102) has published 13 new species of the genus Cornus, chiefly from China. E. HACKEL (*ibid.* 153–161), under the title *Gramineae novae V*, has published 8 new species and 5 varieties of grasses from Bolivia. E. L. GREENE (*ibid.* 161) records a new species of Argemone from New Mexico. E. ROSENSTOCK (*ibid.* 175), in an article entitled *Filices novae IV*, has published 4 species and one variety of ferns as new to science. B. P. G. HOCHREUTINER (Ann. Conserv. et Gard. Genève **11–12**:136–143, reprint pp. 1–8. *pls. 1, 2.* 1908) has published a revision of the genus Adansonia in which 8 species are recognized, one of which, *A. Stanburyana* from northwestern Australia, is proposed as new to science. G. A. NADSON (Bull. Jard. Imp. Bot. St. Petersb. **8**:113–121. *pl. 1.* 1908) describes a new microorganism (*Rhodosphaerium diffluens*) from the Caspian Sea; the systematic position of the plant according to the author is "an der Grenze zwischen Algen und Bakterien." C. FERDINANDSEN and O. WINGE (Bot. Tidsskr. **29**:1–25. *pls. 1, 2.* 1908) have published 19 new species of fungi; these are based on collections made in the Danish West Indies by C. RAUNKIAER during the years 1905 and 1906. W. FAWCETT and A. B. RENDLE (Journ. Botany **47**:3–8. 1909) have published diagnoses of 12 new species of orchidaceous plants from Jamaica; these are preliminary to a monograph of the orchids of Jamaica. E. ULE (Engl. Bot. Jahrb. **42**:191–238. 1908), in collaboration with different specialists, under the title *Beiträge zur Flora von Bahia I*, has published 75 species and one variety as new to science; these are referred to families in the Engler sequence from the Bromeliaceae to the Araliaceae and include the following new genera: *Sincoraea* and *Cryptanthopsis* (Bromeliaceae), *Heptocarpum* (Capparidaceae), and *Itatiaia* (Melastomaceae). E. KOEHNE (*ibid.* Beiblatt 97:47–53) records 5 new species and 4 new varieties in the Lythraceae from South America, Africa, and Siam. Different authors (Kew Bull. **1908**:432–441), under the title *Diagnoses Africanae XXVI*, have published 19 new species and one variety of African angiosperms, including 2 new genera (*Aristogeitonia* and *Androstachys*) of the Euphorbiaceae; also (*ibid.* 445–451) in *Decades kewensis: Decas LI*, 10 new species are described from various localities. E. L. GREENE (Leaflets Bot. Obs. & Crit. **2**:1–24. 1909) proposes a series of 60 new species and 3 new varieties of flowering plants, chiefly from western United States. J. BORNMÜLLER (Mitt. Thür. Bot. Ver. **23**:1–27. 1908), in continuation of his contributions under the title *Novitiae Florae Orientalis*, has published 23 species as new to science, of which 17 belong to the genus Astragalus. A. SCHERFFEL (Ber. Deutsch. Bot. Gesells. **26a**:762–771. 1909), proposes a new genus (*Asterococcus*) for the alga hitherto known as *Pleurococcus superbus* Cienk. N. L. BRITTON (Bull. N. Y. Bot. Gard. **5**:311–318. 1909), in continuation of his studies on the flora of the Bahamas, has described 6 new species of flowering plants. F. S. EARLE (*ibid.* 373–451), under the title of *Genera of the North American Gill Fungi*, recognizes 147 genera for North America, and of these 38 are designated as new.—J. M. GREENMAN.

Hybrids of Oenothera.—DEVRIES has recently published several remarkable papers on hybridization in Oenothera. The results concern a new type of hereditary behavior, which is of great interest, showing as it does that we are only on the borderland of knowledge in these fields. Such discoveries, which open new vistas for the future, are of special value as a stimulus to research. The first of these papers appeared in this journal[11] and announced the discovery of what are called twin hybrids, and a later paper[12] dealt with triple hybrids. In certain cases, when one of the wild species of the Onagra group is crossed with *O. Lamarckiana* or one of its mutants, two types are produced in about equal numbers, both of which breed true, the same types appearing in the different crosses. These types DEVRIES calls *O. laeta* and *O. velutina*. In the case of *O. scintillans* and *O. lata* triple hybrids are produced—in addition to *O. laeta* and *O. velutina* a third type resembling the mother (*O. lata* or *O. scintillans*), but in its special marks intermediate between its parents.

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[11] DEVRIES, HUGO, On twin hybrids. BOT. GAZETTE **44**:401–407. 1907.

[12] ———, On triple hybrids. BOT. GAZETTE **47**:1–8. 1909.

The twin hybrids of *O. nanella* have been worked out most completely.[13] *O. muricata* × *O. nanella* produces the two types *laeta* and *velutina*, about 50 per cent. of each. The *laeta* breed true for four generations, but the *velutina* split in the F_2 and all succeeding generations, producing *velutina* and something over 50 per cent. of a form called by DEVRIES *O. murinella*, which is a dwarf *O. velutina* and breeds true. The dwarf character (but not the other *O. nanella* characters), therefore, reappears in over half of each generation. The discoveries of greatest interest follow. *O. velutina* × *O. murinella* gives the same results as *O. velutina* self-pollinated, i. e., over 50 per cent. *O. murinella*. From this the conclusion is drawn that the pollen of *O. velutina* has the same hereditary qualities as that of *O. murinella*. The reciprocal cross gave 100 per cent. *O. murinella* (280 plants). The facts are all explained by assuming that the egg cells of *O. velutina* are of hybrid (heterozygote) nature ($a \times b$), while the pollen bears only the dwarf character (a). On self-pollination *O. velutina* would then give 50 per cent. *O. velutina* ($a \times b$) and 50 per cent. *O. murinella* (a) which breed true. This conclusion is verified by crosses of *O. velutina* and *O. nanella* (since *O. velutina* × *O. nanella* gives 57 per cent. *O. murinella*, and *O. nanella* × *O. velutina* gives 100 per cent. *O. murinella*).

Similarly, *O. laeta* crossed with *O. murinella*, *O. nanella*, or *O. velutina* gives 50 per cent. *laeta* and 50 per cent. dwarfs. Therefore the egg cells of *laeta* are also hybrid (heterozygote) in regard to the dwarf character, although when self-pollinated *laeta* breeds true! The pollen of *laeta* therefore bears the hereditary characters for high stature. This dominates over the hybrid nature of its own egg cells, but is recessive to the egg cells of pure dwarfs. The remarkable situation therefore appears, that the egg cells of both *velutina* and *laeta* behave as heterozygotes, while the pollen of the former behaves as though it carried only the dwarf character, and the pollen of *laeta* appears to carry only the character for high stature.

Another paper[14] shows that the hybrids of *O. gigas* behave differently from those of other mutants. *O. gigas* × *O. Lamarckiana* forms a constant intermediate race. *O. Lamarckiana* × *O. gigas*, *O. gigas* × *O. brevistylis*, *O. gigas* × *O. rubrinervis*, and *O. rubrinervis* × *O. gigas* all give the same hybrid race. *O. lata* × *O. gigas*, however, gives two types, about half intermediate between *O. gigas* and *O. Lamarckiana*, and half intermediate between *O. gigas* and *O. lata*. *O. gigas* crossed with *O. biennis* and *O. muricata* produces intermediate sterile hybrids.

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[13] DEVRIES, HUGO, Ueber die Zwillingsbastarde von *Oenothera nanella*. Ber. Deutsch. Bot. Gesells. **26a**:667–676. 1908.

[14] ———, Bastarde von *Oenothera gigas*. Ber. Deutsch. Bot. Gesells. **26a**: 754–762. 1908.

Miss LUTZ[15] studied forty individuals of *O. lata* × *O. gigas* and describes a group of hybrids which probably include both the types of DEVRIES, and in addition plants like *O. lata* and like *O. gigas*, having their respective numbers of chromosomes.—R. R. GATES.

Nitrogen fixation by Azotobacter.—KRZEMIENIEWSKI has contributed a paper[16] that seems to throw much-needed light on the problems of nitrogen fixation by Azotobacter in the soil. Perhaps its most valuable feature is the demonstration of the accelerating influence of humus on the process. He finds that Azotobacter in pure cultures in ordinary nitrogen-free media can fix little atmospheric nitrogen, but that the addition of sterile soil or of humic acids or their calcium, potassium, or sodium salts to such solutions multiplies the amount of nitrogen fixed many times. It is interesting to note further that the humus derived from different soils does not yield uniform results, and that artificial "humus" formed by the action of acids on carbohydrates is of little or no value. LIPMAN[17] in this country has anticipated in part some of these results, for he found that the amount of nitrogen fixed by Azotobacter growing in solutions to which different types of soils had been added varied greatly. KRZEMIENIEWSKI further reaches the interesting conclusion, as a result of repeated experiments, that humus does not serve either as a source of nitrogen or of carbon for Azotobacter. He finds that the various nitrogen compounds used in an effort to duplicate the stimulating influence of humus are without such results. When these compounds were used in conjunction with humus they were found to be even decidedly inhibitory in action. Why the humus should thus stimulate growth of Azotobacter he fails to explain, although he seems to have had abundant experimental evidence of the fact. The author was able to demonstrate as much as seventeen milligrams of nitrogen fixed per gram of glucose used in carbohydrate solutions to which humus or humic acids had been added. This is a higher ratio than has been reported by other investigators. He further succeeded in demonstrating by gas analysis for the Azotobacter what was long ago demonstrated for the legume, an actual decrease in the amount of nitrogen supplied to the culture. The organic nitrogen fixed in the culture solution was found at the close of the experiment to check very closely with the amount which disappeared from the air.

The organism is a strict aerobe, neither alcohols, acids, nor hydrogen gas are found as products of metabolism. The ratio $\frac{CO_2}{O_2}$ approaches unity. The temperature optimum for nitrogen fixation is 28° C. Prolonged cultivation of Azotobacter on artificial media the author finds has little influence on its "virulence" or ability to fix nitrogen. The contradictory results of other investigations are probably due to the use of different strains of organisms. The differences between these strains are varietal or, possibly, even specific, for cultures from various sources differ considerably in their nitrogen-fixing power.

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[15] LUTZ, ANNE M., Notes on the first generation hybrid of *Oenothera lata* × *O. gigas*. Science N. S. **29**:263–267. 1909.

[16] KRZEMIENIEWSKI, S., Untersuchungen über *Azotobacter chroococcum*. Beij. Bull. Acad. Sci. Cracovie Cl. Sci. Math. et Nat. **1908**:299–1050. *pl. 1.*

[17] LIPMAN, JACOB G., Bacteriological indications of the mineral requirements of soils. Ann. Rep. N. J. State Agr. Exp. Sta. **27**:177–187. 1906.

BEIJERINCK in his work on these organisms proposed a theory of symbiotic activity between Azotobacter and other bacteria. KRZEMIENIEWSKI concludes that BEIJERINCK'S results are to be explained not as due to the presence of the second organism but to the addition of humus to culture solutions.

These studies should serve to emphasize further the importance of soil humus from the standpoint of agricultural practice. In addition to the solution of certain puzzling questions, KRZEMIENIEWSKI has opened several very promising avenues for successful and profitable research in soil bacteriology.—ROBERT E. BUCHANAN.

Mutability and variability.—SCHOUTEN[18] has an extensive account of two years' Oenothera cultures. Seeds from DEVRIES, as well as commercial seeds and "wild" seeds, and rosettes of various species were used. Several new mutants appeared, and a number of interesting combination forms possessing the characters of two types are recorded. The new mutants are *O. blanda* and *O. candelabriformis*, while the combination forms include *O. laevifolia brevistylis*, *O. laevifolia nanella*, *O. rubrinervis brevistylis*, *O. rubrinervis lata*, *O. gigas nanella*, and *O. gigas lata* (?).

He makes the suggestion, which appears rather unlikely, that the *nanella* or dwarf condition in *OO. Lamarckiana*, *laevifolia*, and *gigas* may be due to bacterial action. *O. Lamarckiana nanella* is found to exist in two forms, differing in their bud and flower characters. *O. gigas* is well known to show extremely wide variability, particularly in leaf shape, and an attempt was made to segregate several types, but without success, since the offspring from each showed nearly the whole range of variation.

The occurrence of a number of combination types as mutants in pure strains gives a somewhat different appearance to the mutation phenomena in Oenothera. SCHOUTEN concludes that mutants originate by two different methods: (1) When both the gamete nuclei uniting in fertilization have the constitution of the same mutant. (2) When the gamete nuclei are unlike. Of the latter he classifies two sorts. (*a*) When one gamete nucleus has the constitution of the species and the other that of the mutant. (*b*) When both the gametes have a mutant constitution but not of the same mutant, thus accounting for the combination forms. Further evidence is obtained from the fact that crossing increases the production of mutants.

The third part of the contribution deals with statistical studies of variability in *O. Lamarckiana* and its mutants, and in several wild species. The parts measured include the length and breadth of certain stem leaves selected according to a definite rule; the length and breadth of the petals and sepals of certain selected flowers; the number of stigma lobes; the length of style, hypanthium, and ovary; length of main stem; number of side branches, etc. A large number of interesting data of variability are here brought together. It is of interest that in nearly all cases the modal number of stigma lobes shows a decrease from 6 or 8 or more to 4 during the season.

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[18] SCHOUTEN, A. R., Mutabiliteit en variabiliteit. pp. 196. Groningen. 1908.

The work is an extension of SHULL'S[19] statistical studies. SHULL found that in the characters measured, the mutants of *O. Lamarckiana* are more variable than the parent form, and hence that phylogenetically younger forms are probably more variable than the phylogenetically older. This appears to hold for the European *O. biennis* and its mutants *cruciata* and *sulfurea*, but is only partly true for *O. Lamarckiana* and its mutants. *O. gigas* and *O. rubrinervis lata* are more variable than the parent in all the organs examined; but the other mutants are more variable in some characters and less so in others. The coefficient of variability of a mutable species is not markedly different from that of a non-mutable form.—R. R. GATES.

Ontogenetic theory of alternation.—LANG[20] has outlined an interesting theory of alternation of generations which he calls an "ontogenetic" theory, to distinguish it from other theories. The so-called "homologous" and "antithetic" theories are well known, and LANG's work on apogamy in ferns inclined him to accept the former. In fact, the ontogenetic theory is a theory of homologous alternation in its phylogenetic application.

The author starts with the idea that all the cell progeny of a germ cell are potentially similar, and that any one of them might reproduce the organism. The development of a specific organism is regarded as due to the properties of the germ cell and to the conditions under which the germ cell develops. The author, therefore, reaches the conception of a specific cell corresponding to each specific form, to which under normal conditions it gives rise. In plants with a definite alternation of generations, germ cells capable of developing into an organism are met twice in the life-history. The organisms developed by these two cells may be very similar or very different. For example, in Polysiphonia the two resulting organisms are very similar; while in bryophytes and pteridophytes they are very different. To explain the latter case the author recognizes two alternative views: (1) the two germ cells are so different that they necessarily produce different structures; (2) the two germ cells are both specific cells of the same plant, but the conditions of development are so different that the two resulting organisms are very different.

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[9] MACDOUGAL, D. T., *et al.*, Mutants and hybrids of the Oenotheras. Pub. No. 24, Carnegie Institution. p. 57. *figs. 13. pls. 22.* 1905; Mutations, variations and relationships of the Oenotheras. Pub. No. 81, Carnegie Institution. pp. 92. *pls. 22. figs. 73.* 1907.

[20] LANG, W. H., A theory of alternation of generations in archegoniate plants based upon the ontogeny. New Phytol. **8**:1–12. 1909.

The second alternative is the basis for the proposed ontogenetic theory of alternation, the assumption being that the two germ cells of a life-history, although one is haploid and the other diploid, have potentially the same morphogenetic properties, and under the same conditions would produce similar structures. In the case of the very dissimilar generations of bryophytes and pteridophytes, the causal differences in the conditions of development are expressed broadly as follows: the spore develops free, in direct relation to soil, water, light, etc.; the fertilized egg develops in relation to the body of the sexual generation. The egg is thus removed from all the influences acting on the spore, and is exposed to a new set of nutritive and "correlative" influences proceeding from the parent body. Since each stage in the ontogeny is probably determined by the preceding stage, the general structure of the resulting organism is as fully determined by the relatively short association of egg and gametophyte among pteridophytes, as by their much longer association among bryophytes.

It is evident that this theory regards the two generations of each species as homologous, in that they are developed from germ cells with the same morphogenetic powers. The really important comparisons to make, therefore, are between gametophyte and sporophyte of the same plant; rather than between the sporophyte of ferns and gametophyte of liverworts, for example. The author promises a full discussion of the application of this theory in future papers, but in the present one he gives a very brief outline of its application to ferns, lycopods, and horsetails, comparing the two generations in each group in a most suggestive way. If the chief value of a theory lies in the work it stimulates, this ontogenetic theory should prove of great value, for it opens a large vista of experimental work.—J. M. C.

Morphology of Ruppia.—GRAVES[21] has investigated *Ruppia maritima* in all its aspects, presenting under the title of morphology, not only the gross and minute features of its morphology, but also its anatomy, ecology, and physiology. Such a compendium of statements in reference to a single species is unusual, for in general an investigator in these days is compelled to restrict his attention to one aspect of plants. For this reason, it is impossible for the reviewer to recognize the contributions to knowledge that must be imbedded in the general account, except in a somewhat restricted division of morphology. The general outline of topics is as follows: Morphology of the vegetative organs (46 pp.), in which the structure and function of stem, leaf, and root are described in great detail and contrasted with those of other Potamogetonaceae; Ecology of the vegetative organs (13 pp.), in which the hydrophytic and halophytic adaptations are presented, and the difficult problem of adaptation and heredity discussed; Reproductive organs (18 pp.), in which flower, sporangia, gametophytes, fertilization, and endosperm are described; Embryo; Fruit and seed; Seedling. The paper closes with two summaries and a bibliography of 98 titles.

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[21] GRAVES, A. H., The morphology of *Ruppia maritima*. Trans. Conn. Acad. Sci. **14**:59–170. *pls. 1–15. figs. 33.* 1908.

Some of the ecological results are as follows. Ruppia is called a water halophyte, living in salt water that would produce plasmolysis in fresh-water plants, but unable to live in water of the open ocean. The hydrophytic responses of the shoot are the weak and spreading form, the absence of stomata, the production of slime, the numerous air spaces, the lack of mechanical tissue, and the reduction of the vascular system to one axial bundle and two lateral ones in both stem and leaf. The responses of the root are a reduction of the system to small unbranched roots borne singly at the nodes, the presence of air spaces, and the concentric axial bundle. The axial and cortical bundles are thought to be useless hereditary structures.

Some of the facts in reference to the reproductive structures are as follows. The inflorescence is a reduced spadix, and a small spathe is present, which is said to have escaped the notice of investigators almost entirely. In the development of the microsporangium a large archesporial group of cells is differentiated, which later becomes septate. In the development of the megasporangium, usually only one layer of parietal cells is formed, and in one case two functioning mother cells were observed in a sporangium. The count of chromosomes was made in the microsporangium and in the reduction divisions of both gametophytes, and was found to be eight and sixteen. The male cells are produced before pollination, which is accomplished by means of the water. The endosperm is scanty, never being more than a thin layer lining the sac. The proembryo is a filament of three or four cells, the basal one becoming much enlarged to form the suspensor. The three embryo-forming cells produce at first a spherical group of cells, and it is believed that both cotyledon and stem tip are derived from the terminal cell of the proembryo, the two other cells producing the hypocotyl, adventitious root, and primary root, the last organ never functioning.

The paper contains a large amount of information in reference to a very interesting form, and the plates, some of them photomicrographs, reproduce the structures in such a way that every botanist can make his own interpretations. —J. M. C.

Orchid flowers and formative stimuli.—As a product of his visit of three months at the Buitenzorg Garden, FITTING published in the initial number of the new *Zeitschrift für Botanik* an account of his experiments on the effect of pollination and other stimuli upon the postfloration behavior of the flowers of orchids.[22] The tropical orchids, available in great abundance at this garden, are especially suited for experimental study on this point, because the difference in duration of pollinated and unpollinated flowers is sufficient to give opportunity for experimentation with unequivocal results, whether the postfloration processes are autonomous or induced. Of these processes he distinguishes four: (1) premature fading; (2) closure of the stigma and swelling of the gynostemium; (3) swelling of the ovary; (4) greening of the perianth.

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[22] FITTING, H., Die Beeinflussung der Orchideenblüten durch die Bestäubung und durch andere Umstände. Eine entwickelungsphysiologische Studie aus den Tropen. Zeits. Bot. **1**:1–86. *figs. 27.* 1909.

He was able to induce premature fading by applying most various substances to the stigma: besides their own living pollen, volcanic river-sand, spittle, dead pollen and pollen extract, dead and leached pollen of the same species or of other genera or even of other and remote groups, and extract of gynostemium tissues induced it, and apparently also 5 per cent. saccharose. He was not able to determine what the chemical agent or agents were in these reactions. Wounding the stigma or the tissue at the apex of the gynostemium also caused premature fading. Closure of the stigma and swelling of the gynostemium could be effected by bestrewing the stigma with living or dead pollen of orchids (any genus) or even of Hibiscus, and with the alcoholic extract of pollen. On the contrary, dead pollen and pollen extract had no effect or the very slightest in inducing swelling of the ovary, which occurred only when living pollen germinated on the stigma and its tubes grew into the ovary. The greening of the perianth (peculiar to certain species) appears only when the ovary has previously begun to swell and to turn green.

FITTING considers fading as the end process of floral development, simply released by the pollen stimulus or others earlier than it is autonomously. The stimulus, however, does not merely hasten development; it diverts its course, for a perianth half open and quite incompletely developed may be made to fade in twelve to twenty-four hours by a stimulus which proceeds from the distant stigma. This also offers a new example of the separation of perceptive and reactive regions. The closure of the stigma, etc., appears to be strictly a case of chemomorphosis, but the agent does not produce any effect on the ovary, whose growth and formation of ovules, and so the consequent greening of the perianth, depend on the penetration of the pollen tube; but whether the stimulus is mechanical or chemical does not appear.

The prompt fading of the flowers, possible after an insect bite on the stigma or after stimulation by foreign pollen, and the small crop of fruit on these tropical orchids, awaken doubts in FITTING'S mind as to the validity of the teleological interpretation of the elaborate mechanisms which are believed to secure cross-pollination. Perhaps they were effective in a past age when insect life was richer, he adds by way of apology for his temerity in suggesting such heresy. He will find this heresy not unwelcome, we imagine, in this country, where ecologists are questioning whether there is even adequate proof that cross-pollination is advantageous.—C. R. B.

Cytology of Oenothera.—GEERTS[23] published an account of embryo-sac development and chromosome reduction in Oenothera. A row of four megaspores is formed, with typical reduction phenomena, the megaspore nearest the micropyle forming the embryo sac. Its nucleus divides only twice. Both nuclei resulting from the first division remain in the upper portion of the sac. One of these divides to form the two synergids, and the other forms the egg and polar nucleus. There are therefore no antipodals and only one polar nucleus. In fertilization one male nucleus unites with the egg; the other unites with the polar nucleus to form the endosperm.

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[23] GEERTS, J. M., Beiträge zur Kenntnis der cytologischen Entwicklung von *Oenothera Lamarckiana*. Ber. Deutsch. Bot. Gesells. **26a**:608–614. 1908.

———, Beiträge zur Kenntnis der Cytologie und der partiellen Sterilität von *Oenothera Lamarckiana*. Separate (source unknown). pp. 116. *pls. 5–22.* 1909.

The account of reduction phenomena confirms, in all the main points, the previous accounts of GATES.[24] There is no fusion of parallel threads in synapsis. The spirem later breaks into the vegetative number of chromosomes, which afterward become paired. The first mitosis separates whole chromosomes, and the second separates the longitudinal halves of these. Certain critical stages during the period between synizesis and diakinesis, which prove that the chromosomes are formed by the segmentation of a single spirem thread, are not represented; but these stages are the most difficult to obtain, probably because they are passed through quickly. It seems now pretty evident that there are two general methods of reduction in plants, as in animals, one involving a telosynapsis, the other a parasynapsis or side-by-side pairing of chromosomes.

The question of sterility is also examined, with interesting results. In *Oenothera Lamarckiana* 50 per cent. of the ovules are found to degenerate, and about 50 per cent. of the pollen grains—two from each tetrad of spores. A large number of other Onagraceae were examined, nearly all of which were found to exhibit more or less sterility. GEERTS concludes that the sterility of *O. Lamarckiana* cannot be explained as the result of hybridization, cultivation, or lack of nutrition or space, but that it has been inherited from a remote ancestor, probably from the ancestor of the whole sub-family. He thinks that since this sterility is heritable it must have originated by a mutation, or rather two mutations, one on the pollen side and one on the megaspore side, since they are often sterile in different degrees in the same species!

So far from explaining anything, it seems to the reviewer that this muddies the pool and is much worse than a flat confession of ignorance as to the cause. It will be unfortunate if botanists acquire the habit of ascribing the origin of complex conditions, such as sterility, to a sudden "mutation" in some ancestor. There is no evidence to show that the sterility has not been gradually acquired, and for that matter independently acquired, in the different species. To call it a mutation helps to explain neither its origin nor its cause.—R. R. GATES.

Seedlings of conifers.—HILL and FRAINE[25] have published a second paper on the seedlings of gymnosperms, the thesis being that polycotyledony is attained by the splitting of preexisting members, which were probably two in number. In the present investigation seedlings of Tsuga, Abies, Picea, Cedrus, Pinus, Larix, Pseudolarix, and Araucaria were studied. The general result shows that the Taxineae, Podocarpineae, and many Cupressineae have two cotyledons, and that each cotyledon (Podocarpineae being excepted) contains one vascular strand and the primary root is diarch. Among the Abietineae, however, in which polycotyledony prevails, each cotyledon has a single vascular strand, but the number of poles of the primary root holds no obvious relation to the number of cotyledons.

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[24] GATES, R. R., A study of reduction in *Oenothera rubrinervis*. BOT. GAZETTE **46**:1–34. *pls. 1–3.* 1908.

[25] HILL, T. G., AND DE FRAINE, E., On the seedling structure of gymnosperms. Annals of Botany **23**:189–227. *pl. 15. figs. 11.* 1909.

In summarizing the evidence of splitting, the authors add the following testimony: the occurrence of partially split cotyledons, the frequent obvious grouping of cotyledons, and the cases of transition. *Pinus contorta Murrayana* may be selected as an illustration of the last case, in which form three entire cotyledons were found, one of them much larger than the other two and containing two entirely distinct vascular strands. The authors speak of this as a case of one whole cotyledon and two half-cotyledons. Trouble of course comes with the higher numbers of cotyledons, and at this point the explanation offered is not clear. It is acknowledged that in some cases an increased number of cotyledons may result from the appearance of extra primordia, which represent the displacement of foliage leaves from the first stem node to the cotyledonary node.

The general summary of facts contains the following items: the occurrence of more or less complete cotyledonary tubes (over 20 species cited); the existence of cases of incomplete splitting (4 species cited); the general presence of cotyledonary resin ducts (several in araucarians, two in 12 species cited, one in 6 species, and none in 6 species or more); the occurrence of 4–8 vascular strands in each cotyledon of Araucaria, and of one strand in the cotyledons of Tsuga, Abies, Picea, Cedrus, Pinus, and Larix; the occurrence of mesarch structure in occasional cotyledons of *Tsuga canadensis*, *Pinus Pinea*, and *P. Gerardiana*.

SHAW[26] has investigated the seedling of *Araucaria Bidwillii*, a tuberous species and one not studied by HILL and FRAINE. He finds that the cotyledonary vascular strands are very numerous and variable (12 to 16), that the poles of the root are equally variable (5 to 7), and that there is a very confused connection between the two. The protoxylem groups of the root are gradually reduced until the diarch condition is finally attained.—J. M. C.

The Piccard rotation experiments.—HABERLANDT[27] has repeated PICCARD'S rotation experiments,[28] for which he used the seedlings of *Vicia Faba*, *Lupinus albus*, and *Phaseolus multiflorus*. He characterizes PICCARD'S conception as good, but the execution of the experiments and the interpretation of the results as faulty.

He claims to have eliminated all PICCARD'S technical errors by devising a very substantial and accurate centrifuge, and by securely fastening the seedlings with plaster of Paris, at the same time supplying them with sufficient moisture. The roots were placed at an angle of 45° with the axis, as were PICCARD'S. While PICCARD used 20–40 rotations per second, HABERLANDT found it necessary to use only 5–20.

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[26] SHAW, F. J. F., The seedling structure of *Araucaria Bidwillii*. Annals of Botany **23**:321–334. *pl. 21. figs. 6.* 1909.

[27] HABERLANDT, G., Ueber die Verteilung der geotropischen Sensibilität in der Wurzel. Jahrb. Wiss. Bot. **45**:575–600. 1909.

[28] PICCARD, AUGUST, Neue Versuche über die geotropische Sensibilität der Wurzelspitze. Jahrb. Wiss. Bot. **40**:94–102. 1904.

If the tips of the roots extended 1.5^{mm} or more beyond the axis, they always bent in the direction according with the irritability of the tip; if 1^{mm} or less, the curvature was determined by the irritability of the growing zone. HABERLANDT points out (what he says PICCARD and his critics have failed to notice) that where the root tip extends 1.5^{mm} beyond the axis, the growing zone receives on the average greater stimulation than the root tip, the centrifugal acceleration of the growing region, by reason of its greater length, being 2.8–3.9 times that of the tip. This, of course, is due to the considerable length of the growing zone. HABERLANDT never gets the S curve described by PICCARD. He concludes that 1.5–2^{mm} of the root tip, in the forms worked with, is very sensitive to gravity and to centrifugal acceleration. The growing zone is likewise sensitive, but far less so than the tip. The marked geotropic sensitiveness of the tip corresponds to the well-developed statolith apparatus of the cap, while the slighter sensitiveness of the growing zone is due to the rather poorly developed statolith starch of the periblem in that zone.

He finds that the geotropic irritability of the growing zone is manifested with acclerations as low as 0.25 gravity, and therefore that it comes into play in ordinary geotropic response, exactly opposite to NĚMEC'S conclusion.

HABERLANDT also conducted a set of decapitation experiments, making full allowance for the shock effect of decapitation, which accord fully with the results by the PICCARD method. He concludes that all these results are quite in harmony with the statolith theory.—WM. CROCKER.

Plant proteases.—VINES has now for more than ten years devoted his attention to the proteases of plants and he has made the field practically his own. The conclusions he has from time to time announced mark periods in the development of the problem. The last paper by this author[29] should be considered in two parts, the first of which deals with his latest results, while the second constitutes a review of the earlier investigations, together with final conclusions.

The papain or papayotin of the latex of papaw, which has long been known to digest proteins, was shown by MARTIN to be both peptic and peptolytic. It was therefore designated a tryptic enzyme. The discovery that other vegetable extracts (germinated lupin, castor-bean, some fruit juices, malt, yeast) had a like action, led to the notion that plant proteases in general are tryptic. This conception, although a generalization from too limited data, was an advance, as it supplanted the prevalent idea (also resting upon an insecure foundation) that plant proteases are peptic. Following up his work on tryptic extracts from various sources, VINES has finally come to believe that the proteases of plants are of two sorts, the peptases and the ereptases. This conviction has been further fixed by his latest results, which are that from papayotin both peptase and ereptase may be obtained. The former is soluble in dilute NaCl and little soluble in distilled water, while the latter is easily soluble in pure water. That the demonstration of these two proteases in papayotin might be more complete is admitted by the author. Similarly, preparations from both fresh and dry yeast show the presence of peptase and ereptase.

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[29] VINES, S. H., The proteases of plants. VI. Annals of Botany **23**:1–18. 1909.

The proposal of VINES, after reviewing the subject, to supplant the "vegetable trypsin" idea by the conclusion that the proteases of plants belong to two main groups, the peptases and the ereptases, and his further classification of the former into endopeptases and ectopeptases, appeal to the reviewer as unnecessary and unwarranted, inasmuch as the new may prove to be as incomprehensive as was the "trypsin" idea. Further, if a name must be given to something of which little is known, that name should have some reference to the qualities marking individuality, rather than to the mere incident of its occurrence. So far, the "ectopeptase" is confined to Nepenthes. The anticipation of the author that "ectopeptase" is of wide occurrence may be justified, but in one case, namely, the pitcher-liquid of Sarracenia, peptic action has not been found.[30]—RAYMOND H. POND.

Morphology of Pseudotsuga.—The investigation of the North American representative of this interesting genus by LAWSON[31] has filled a gap in our knowledge. In general it conforms to the well-known characters of Abietineae, but it presents some interesting peculiarities. The pollen grains are wingless, and the mechanism for receiving them is most unusual. There is a stricture of the integument above the nucellus, which results in two distinct micropylar chambers. The outer chamber is partially inclosed by the infolding tip of the integument, from whose inner face numerous hairlike processes are developed as outgrowths from the epidermal cells. Within this chamber the pollen grains are received and germinate, a tangle of tubes passing down through the inner chamber to the nucellus.

At the time of pollination (April–May in California) the pollen grain contains the two disorganized prothallial cells and the generative and tube nuclei. Just before tube-formation the generative cell divides to form the stalk and body cells, both with distinct membranes, but soon becoming very unequal. Before the tip of the nucellus is reached by the tube, the nucleus of the body cell divides to form two unequal male nuclei. Fertilization takes place within 60 days after pollination, and the entire nuclear contents of the tube are discharged into the egg.

The functioning megaspore is surrounded by a distinct tapetal zone, and the magaspore membrane becomes conspicuous. The development of the female gametophyte proceeds as usual, filling the sac with primary endosperm cells, in which free nuclear division occurs before cross-walls form the permanent tissue. The archegonia are usually four in number, and a distinct ventral canal cell is cut off, the membrane persisting until fertilization occurs. The proembryo is the usual one of Abietineae, walls appearing at the eight-nucleate stage, and four tiers of cells being organized, the uppermost tier being open.—J. M. C.

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[30] ROBINSON, WINIFRED J., A study of the digestive power of *Sarracenia purpurea*. Torreya **8**:181–194. 1908.

[31] LAWSON, A. A., The gametophytes and embryo of *Pseudotsuga Douglasii*. Annals of Botany **23**:163–180. *pls. 12–14.* 1909.

Embryo sac of Pandanus.—CAMPBELL[32] has published the details of the development of the embryo sac of this interesting form, the preliminary account having been published last year.[33] The stage showing fertilization was not obtained, so that it is not certain that the fourteen-nucleate condition described is the fertilization stage. The megaspore mother cell is overlaid by several layers of parietal cells, which are thought to be derived from a single cell. The division of the mother cell is followed by the direct production of the embryo sac by the inner daughter cell. At the first division, the two nuclei assume the polar positions, and subsequent divisions result in two micropylar nuclei and twelve antipodal nuclei. If two megaspore nuclei are supposed to enter into the structure of this sac, there is a single division of one of them, and a succession of divisions from the other one. From any point of view, such a sac would be unusual, and the author is inclined to regard it as "a new type with its nearest analogue in Peperomia," a type which is probably more ancient than the prevailing eight-nucleate sac. He dissents from the idea that the reduction division necessarily determines a megaspore in angiosperms, believing that this event may so shift in the life-history that a megaspore may be defined regardless of it. After all, this is merely a matter of definition, and that is a matter of agreement. Shall a megaspore be defined as the product of the two reduction divisions or as the cell which produces the embryo sac? Which definition will have the greater morphological stability?—J. M. C.

Diffusion of CO_2 in leaves.—That CO_2 does not diffuse extensively through the mesophyll has been known for more than thirty years from the researches of MOLL, and experiments to show the localization of photosynthesis have become common in every physiological laboratory. Under MOLL's direction, ZIJLSTRA has investigated the extent of diffusion in leaves of different structures.[34] He finds that in all leaves the CO_2 formed in the leaf itself suffices to produce a line or zone of starch at the edge of the darkened region. In net-veined leaves the movement of CO_2 supplied from the air is prevented by the larger veins which stretch from surface to surface without intercellular spaces. Consequently the width of the lines of starch produced at the edge of the darkened region is not widened even though the unlighted area is supplied with CO_2 under abnormal pressure. If the net be coarse the zone of marginal starch will be wider than if it is fine. Diffusion of self-produced CO_2 to 2.5^{cm} at most is thus possible; for in parallel-veined leaves of Triticum, Hordeum, and Zea, though the veins do not prevent diffusion, the intercellular passages are so narrow as to limit it to 3^{cm}. In Tradescantia and Acorus the transverse anastomoses prevent more extensive movement. In Eichhornia, Pontederia, and Eucomis the leaves have spacious intercellular passages, and so the movement is much more free. But even here the diffusion scarcely surpasses 3^{cm}, unless through a region of the leaf that is not in condition to act on the CO_2. In nature, therefore, movement of CO_2 may be considered practically nil.—C. R. B.

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[32] CAMPBELL, D. H., The embryo sac of Pandanus. Bull. Torr. Bot. Club **36**:205–220. *pls. 16, 17.* 1909.

[33] CAMPBELL, D. H., The embryo sac of Pandanus. Preliminary note. Annals of Botany **22**:330. 1908.

[34] ZIJLSTRA, K., Kohlensäuretransport in Blättern. Proefschrift ter verkrijging aan der graad van Doctor in plant- en dierkunde aan der Rijks-Universiteit te Groningen. . . . . 8vo. pp. 128. *pls. 2. figs. 2.* Groningen: M. de Waal. 1909.

Seedling of a graft-hybrid.—Certain branches of the graft hybrid, *Cytisus Adami*, revert, producing flowers having the characters of the reputed parents *C. Laburnum* and *C. purpureus* respectively. The *C. Adami* flowers are ordinarily sterile, while those borne on reverted branches reproduce their respective parents.

In May, 1904, HILDEBRAND[35] observed that several flowers of a *C. Adami* branch of a cultivated specimen in the Freiburg botanical garden had set seed, and was able to obtain three fruits from them, which had chiefly the characters of *C. Laburnum*, but in certain respects resembled *C. purpureus*. It is not known whether these flowers were self-pollinated, but it is not unlikely that the pollen came from *C. Laburnum* flowers, since the *C. Adami* flowers are usually sterile. Two of the seeds germinated. Both were very similar in character to *C. Laburnum* and in 1907 one of them produced hundreds of flowers, all having the characters of *C. Laburnum*. No conclusions can be drawn regarding the hereditary bearing of these facts, in the absence of a knowledge of the manner of pollination of the flowers and the nature of the next generation of offspring.—R. R. GATES.

Chlorophyll.—The discussion as to the phosphorus content of chlorophyll waxes warm. STOKLASA replies vigorously[36] to TSWETT'S criticisms[37] and takes issue with WILLSTÄTTER'S results.[38] The question is yet in the stage of polemic discussion and will doubtless require further and most careful work. Stoklasa is particularly emphatic, declaring that "we have determined—not only I, but my collaborators, at different times—by definite researches, which we are ready to repeat in any forum, that preparations of chlorophyll all actually contain phosphorus." And again: "Our new investigations, carried out in my laboratory both on crude and pure chlorophyll, prove that the phosphorus is bound up in the chlorophyll complex and does not occur in ionic form. We have recognized with complete certainty glycerophosphoric acid and cholin. Consequently the assertion of Euler and of Schulze, that the chlorolecithin hypothesis is finally refuted by Willstätter's work, is at least premature."—C. R. B.

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[35] HILDEBRAND, FRIEDRICH, Ueber Sämlinge von *Cytisus Adami*. Ber. Deutsch. Bot. Gesells. **26a**:590–595. 1908.

[36] STOKLASA, J., BRALIK, V., UND ERNST, A., Zur Frage des Phosphorgehaltes des Chlorophylls. Ber. Deutsch. Bot. Gesells. **27**:10–20. 1909.

[37] TSWETT, M., Ist der Phosphor an dem Anbau des Chlorophylline beteiligt? *Ibid.* **26a**:214–220. 1908.

[38] WILLSTÄTTER, R., Zur Kenntniss der Zusammensetzung des Chlorophylls. Liebig's Annalen der Chemie **350**:48–82. 1906.

WILLSTÄTTER, R., UND BENZ, M., Ueber krystallisiertes Chlorophyll. *Ibid.* **358**: 267–287. 1907.

The "germination" of Gnetum.—Hill, in studying *Gnetum Gnemon*,[39] finds that the root and hypocotyledonary axis soon escape from the seed coats, leaving behind, in close connection with the reserve food, a foot or sucker. The cotyledons are at first small, but later enlarge somewhat and do photosynthetic work. An older specimen shows the pronounced rodlike foot in the center of the endosperm. The foot contains vascular tissue.

Hill remarks that the foot develops to a greater extent in Gnetum than in either Tumboa or Ephedra. Comparison with the last genus is certainly astonishing. The reviewer can speak for many of the ephedras of the western world. They do not have a structure in the remotest degree resembling the foot of Gnetum as figured by Hill, nor is there even a rudimentary trace of such a structure.—W. J. G. Land.

Sex of Sphaerocarpus.—Acting upon a suggestion by Strasburger, Douin[40] has carefully examined 81 groups of *Sphaerocarpus terrestris*, taken by chance from material collected at Chavannes. He finds that about 75 per cent. clearly show 2 male plants and 2 female arising from the spore tetrad, whose members cohere usually until germination. The others were mainly explicable by non-germination of one or more spores of a single or double tetrad, or the accidental dissociation of the members of a tetrad. Several cases clearly anomalous were found: one group (from 2 tetrads) of 5♂ and 3♀; another of 3♂ and 1♀; and two others, 1♂ and 3♀. He corrects certain earlier misstatements regarding sporelings, and now specifies differences between juveniles of *S. terrestris* and *S. californicus*, which before he declared indistinguishable.—C. R. B.

Necrosis of the grape.—Vines killed by this disease[41] have usually, in the opinion of the owners, "just died," yet the writer regards it as a serious disease causing a large percentage of damage. In one young vineyard of 14 acres it is estimated 4000 to 5000 vines succumbed. The symptoms are: A trimmed and tied vine that has failed to put out shoots; a vine that has sent forth shoots, the latter dying after a few weeks; shoots and leaves that exhibit dwarfing; blanched and chlorotic leaves; leaves and fruit shriveling and dying in the summer; the presence of fleshy or corky excrescences on the stem, of minute black pimples on a dead spur, or of small reddish-brown spots on the green shoots. The disease is attributed to *Fusicoccum viticolum*, which is described as a new species.—F. L. STEVENS.

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[39] Hill, T. G., The germination of *Gnetum Gnemon* L. Jour. Roy. Hort. Soc. **34**:1, 2. 1908.

[40] Douin, Ch., Nouvelles observation der Sphaerocarpus. Rev. Bryol. **36**:37–41. 1909.

[41] Reddick, D., Necrosis of the grape vine. Cornell Univ. Agric. Exp. Sta. Bull. 263. Feb. 1909.

Origin of plastids.—Without giving any adequate evidence, even in outline, SCHILLER propounds the idea in a preliminary paper[42] (which can have no other purpose than to secure priority, and this ought to be denied in such cases even if the guess proves correct) that the plastids of plant cells arise by the extrusion and fragmentation of nucleoli, whose fragments subsequently grow and change their structure. He "is inclined to the view" that the plant cell is therefore to be looked upon as binucleate, in the sense that the chromatophores correspond to a macro- or yolk-nucleus, a view which has lately been expressed by MOROFF for animal cells.—C. R. B.

Leaf blight.—STEVENS and HALL describe[43] a disease of apple, pear, and quince, whose prominent symptom suggests the name leaf blight. As it is due to *Hypochnus ochroleucus* Noack, they propose the name hypochnose, in conformity to a scheme for making names of diseases by combining euphonically the name of the fungus with the termination *-ose*. The disease resembles fire-blight (bacillose), but only the leaves are affected (no twigs), and they stand erect instead of drooping. The disease prevails in the mountain section of North Carolina, West Virginia, and Alabama, but is probably much more widespread.—C. R. B.

Geoglossaceae of N. A.—The attention of those interested is directed to an elaborate monograph[44] of this family of Discomycetes, allied to the better-known Helvella and Morchella types, as represented on this continent. There are eleven genera, and the original fifty-three species DURAND reduces to forty-two. We have no competence to review the work critically.—C. R. B.

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[42] SCHILLER, JOS., Ueber die Entstehung der Plastiden aus dem Zellkern. Oesterr. Bot. Zeits. **59**:89–91. *figs. 3.* 1909.

[43] STEVENS, F. L., AND HALL, J. G., Hypochnose of pomaceous fruits. Ann. Mycol. **7**:49–59. *figs. 8.* 1909.

[44] DURAND, ELIAS J., The Geoglossaceae of North America. Ann. Mycol. **6**:387–477. *pls. 5–22.* 1908.

GENERAL INDEX

Classified entries will be found under Contributors and Reviews. New names and names of new genera, species, and varieties are printed in **bold-face** type; synonyms in *italic*.

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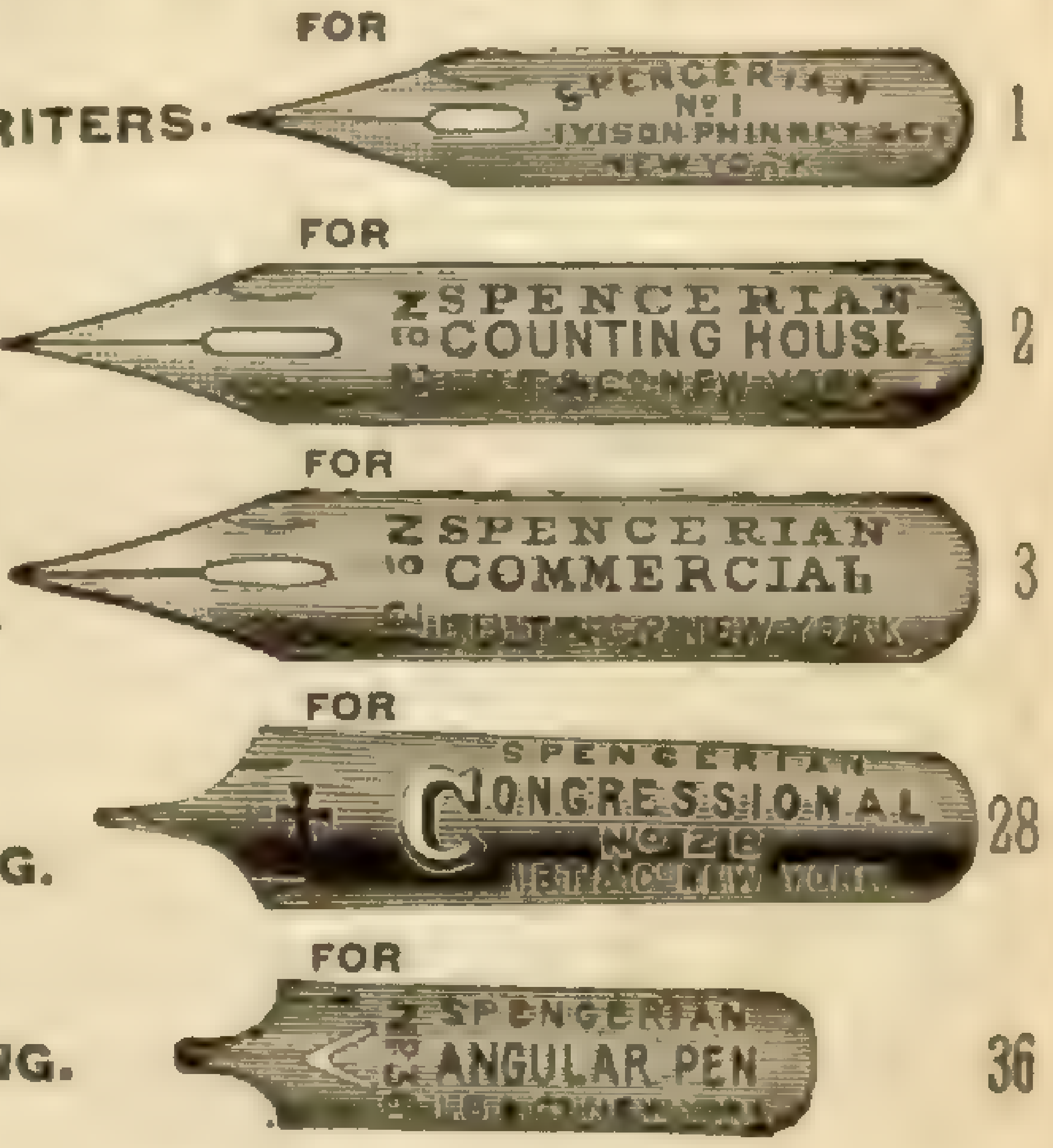

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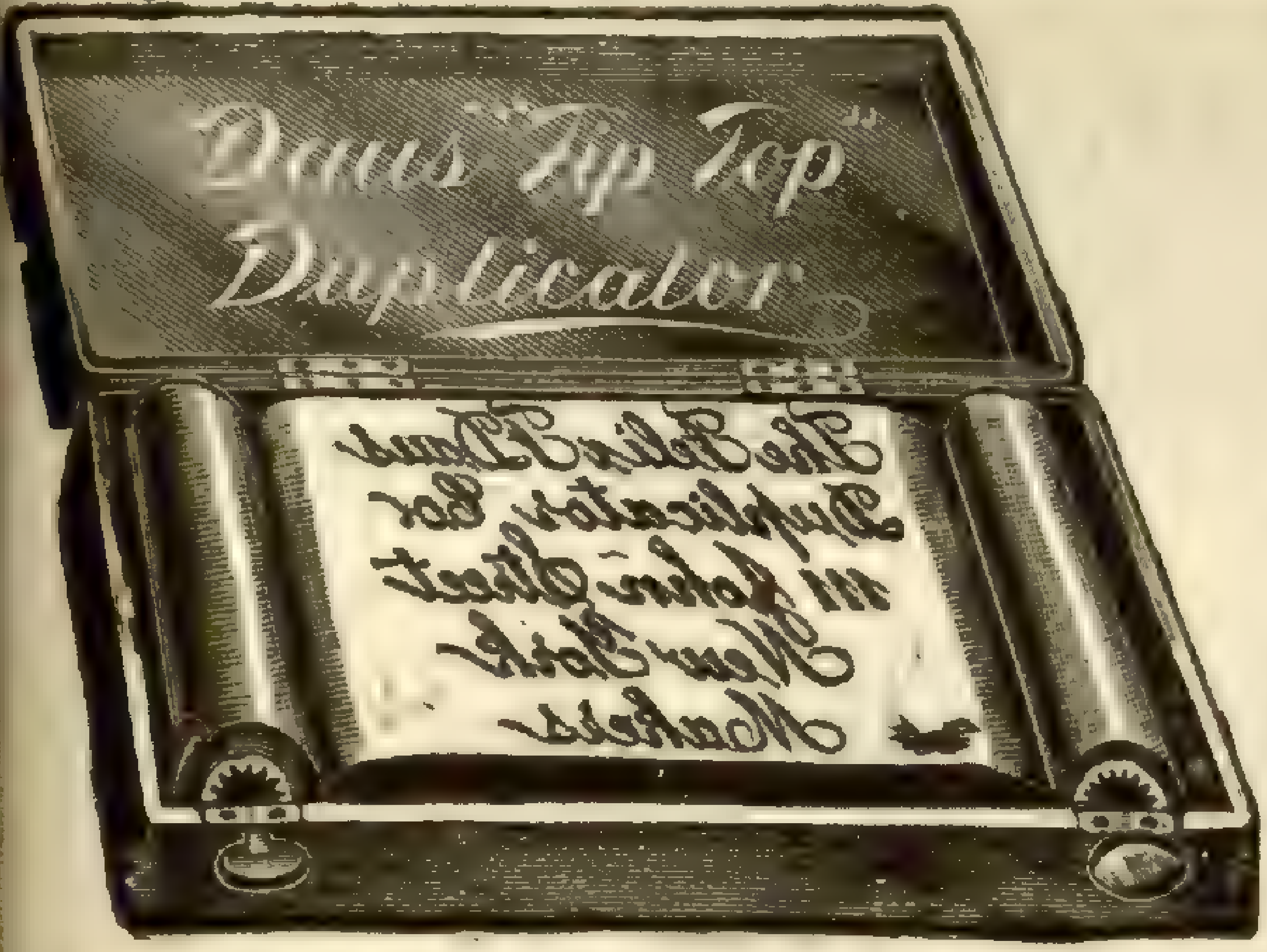

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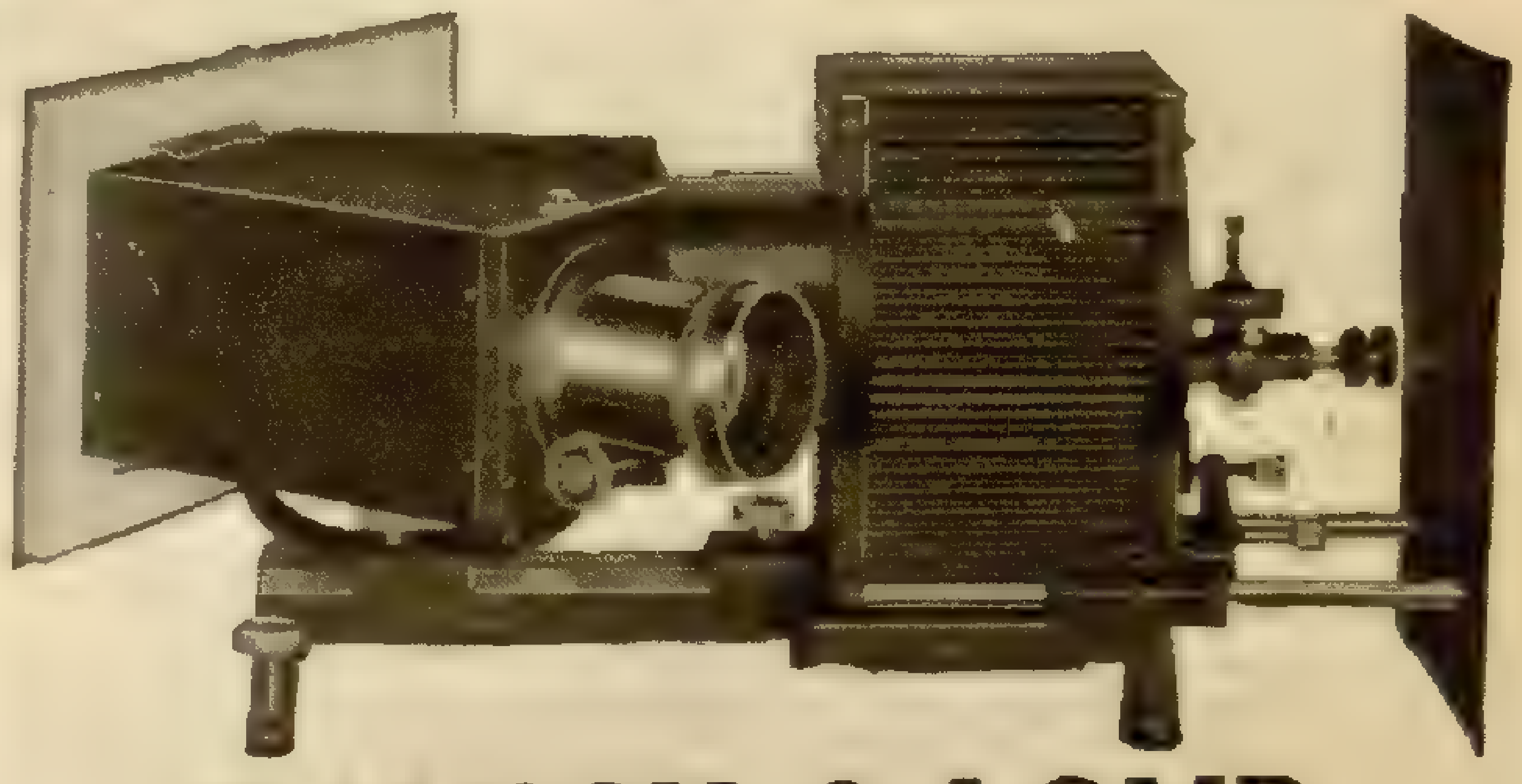

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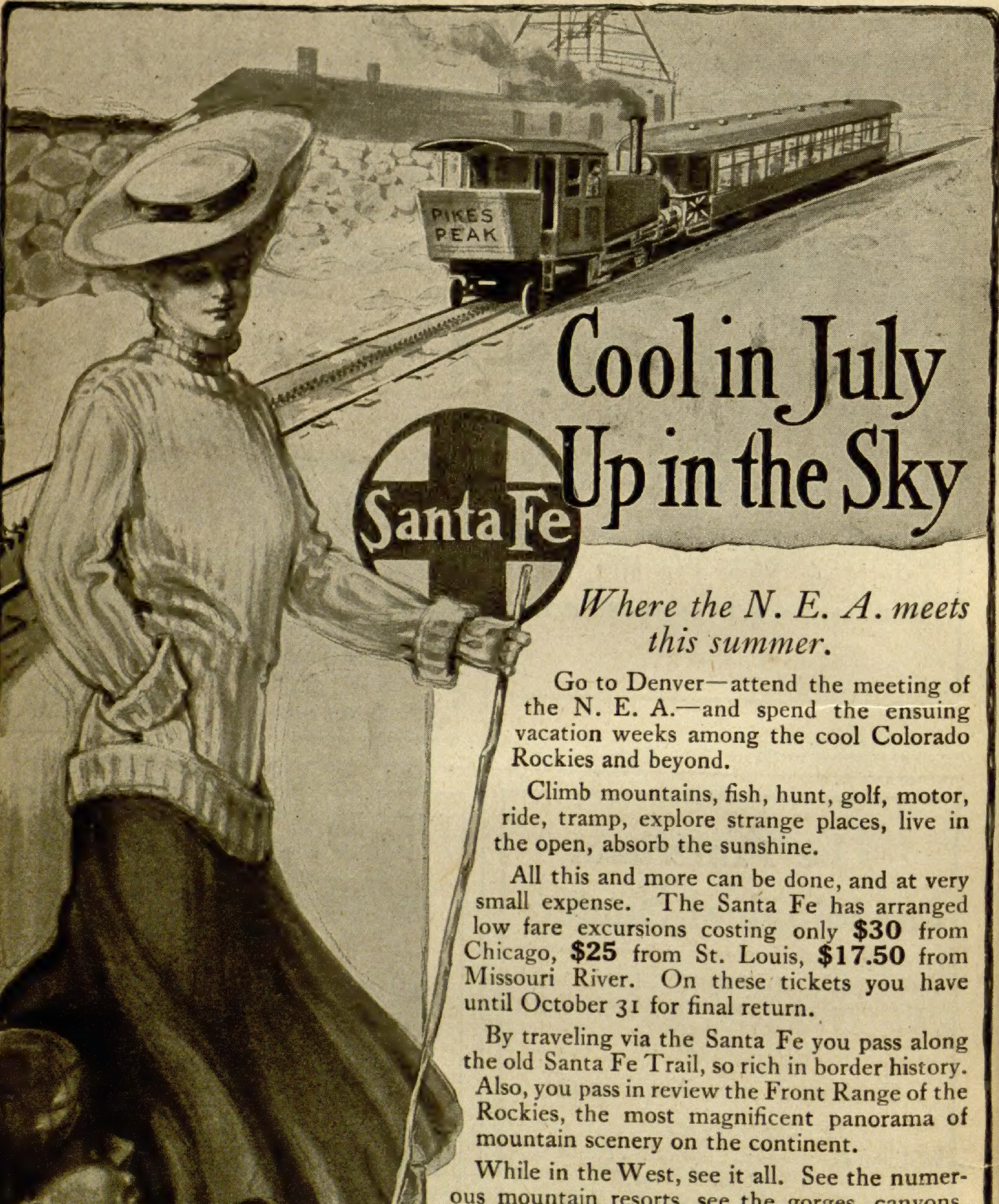

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